A TEXTBOOK OF ZOOLOGY

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A TEXTBOOK OF ZOOLOGY

BY

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CONTENTS

Plate I.

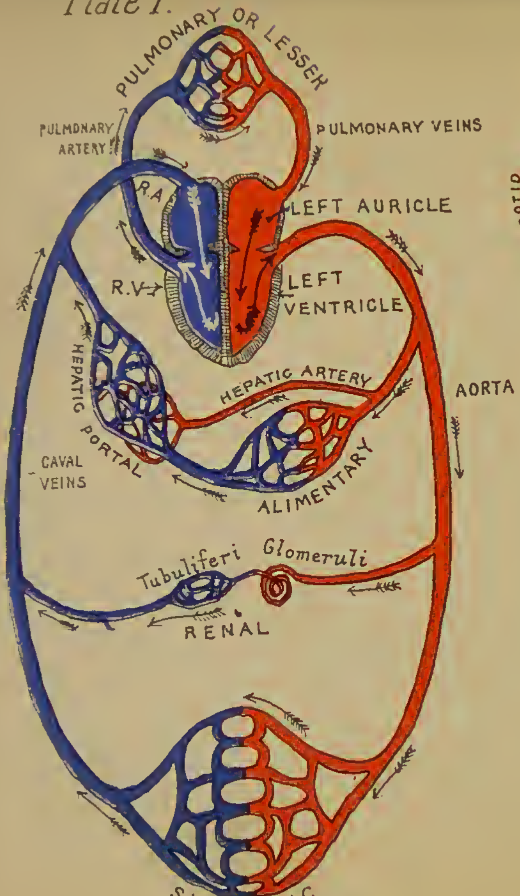

Fig 1, Rabbit.

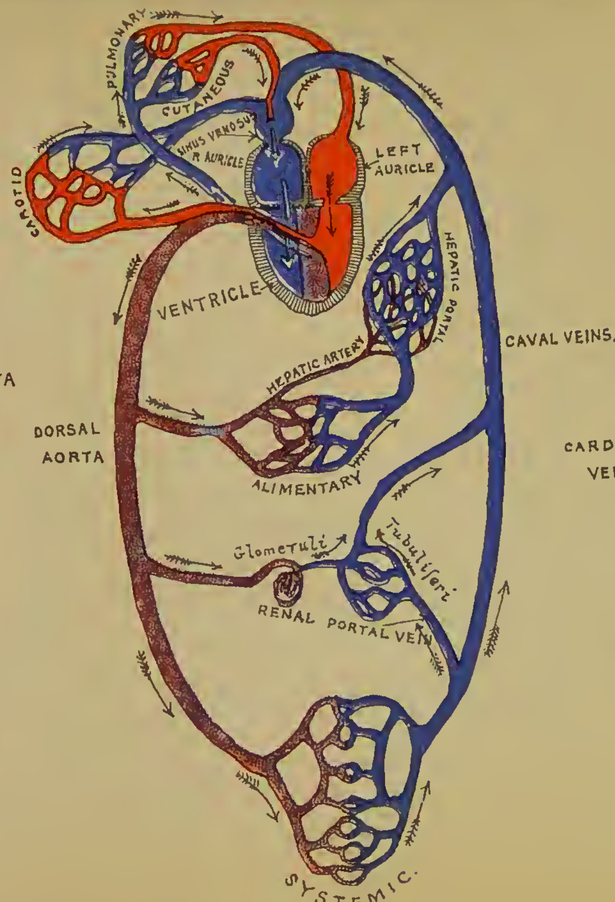

Fig 2, Frog.

Fig 3, Dogfish.

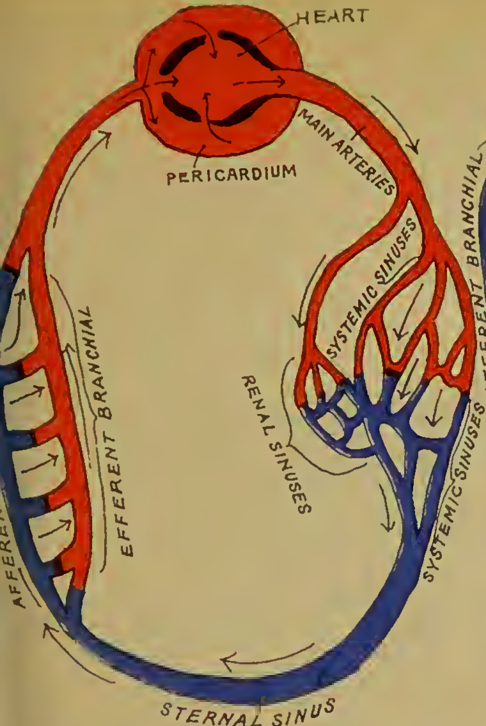

FIG. 1., CRAYFISH

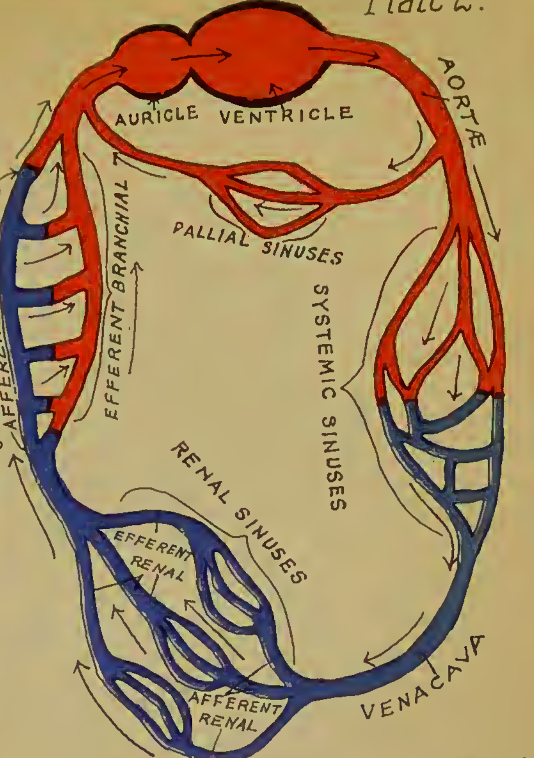

FIG. 2., FRESH-WATER MUSSEL

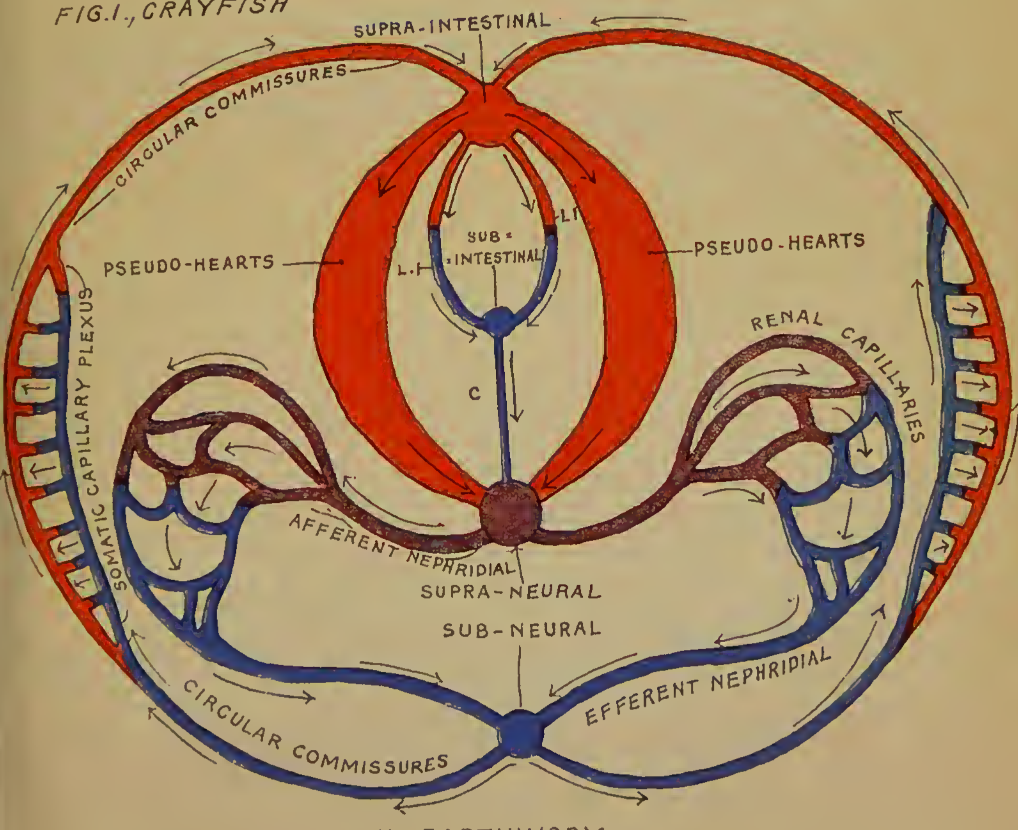

FIG 3., EARTHWORM.

EXPLANATION OF THE PLATES

PLATE I

Fig. 1. Diagrammatic representation of the circulation of the blood in the Rabbit. The arrows indicate the direction of the blood-flow. R.A = right auricle of heart. R.V. = right ventricle. The red colour represents arterial blood, and the blue, venous blood. The groups of network represent the various groups of capillaries and the smaller arterioles and venules.

In all lung-breathing (terrestrial) Vertebrates there is a double circulation of the blood: a Greater or Systemic and a Lesser or Pulmonary (cp. pp. 90–91, 112). The former is the one in the course of which the blood supplies the body, muscles, and the viscera, and the capillaries of which are represented by the biggest network at the bottom of the figure. The capillaries in the wall of the alimentary canal, by their union, form the factors of the hepatic-portal vein, through which the blood is carried to the capillaries of the liver, thence through the hepatic veins to the post-caval vein (cp. p. 110). In the substance of the liver the capillaries derived from the hepatic artery, and which convey arterial blood, become merged with those derived from the hepatic-portal vein, which carry venous and food-product-laden blood.

The renal organs (kidneys) are supplied by the renal arteries, the capillaries derived from them being exclusively confined to the Malpighian capsules, forming little tufts called glomeruli ; the capillaries of the glomeruli are continuous with other sets that ramify over the renal tubules, and which ultimately pour their blood into the renal veins.

Fig. 2. Diagrammatic representation of the circulation of the blood in the Frog. The red colour represents arterial blood, the blue, venous, and the purple, mixed (arterial and venous) blood. By means of the remarkable and simple mechanism of the truncus arteriosus (pp. 85–87) it results that the systemic vessels carry mixed blood, the pulmonary and cutaneous vessels wholly venous blood, and the carotid vessels, supplying the brain and head, wholly arterial blood.

The renal tubules of the frog's kidneys are supplied not only with blood derived from the glomeruli as in the rabbit, but in addition with that brought from the legs by the renal-portal vein (cp. p. 108).

One peculiar result of the skin of the frog serving as a respiratory organ is that the caval veins carry not only venous blood, as in all other Vertebrates, but also a small quantity of arterial blood brought to them by the cutaneous veins.

Fig. 3. Diagrammatic representation of the circulation of the blood in the Dogfish. The red colour represents arterial, and the blue, venous blood.

The blood passing through the heart is wholly venous, and is carried thence to the capillaries of the gills, where it becomes oxygenated. From the gills it passes to the dorsal aorta (p. 93), thence through the systemic and visceral capillaries (cp. p. 104) to the cardinal veins, by which it is returned to the heart.

The renal tubules, like those of the frog, are supplied by blood from the glomeruli and the renal-portal vein (cp. p. 104).

PLATE II

Fig. 1. Diagrammatic representation of the blood circulation in the Crayfish. The red colour represents arterial, and the blue, venous blood. From the heart the major portion of the blood passes to the systemic (including the visceral) sinuses, while a very small portion only passes through the renal organs. All the blood then passes to the great sinus (sternal sinus) in the endophragmal system, whence it traverses the gills, and thence to the pericardial sinus and heart (cp. pp. 238–239).

Fig. 2. Diagrammatic representation of the circulation of the blood in the Mussel. The red colour represents arterial, and the blue, venous blood. From the heart the blood passes through the two aortæ to the system in general, the sinuses of which it traverses, and from which it flows to the vena cava vein. Thence the whole of it passes through the renal organ to the gills, whence it returns to the heart again. A small portion of the blood leaving the aortæ passes at once through the pallial sinuses and thence is carried direct to the heart (cp. p. 242).

Fig. 3. Diagrammatic representation of the blood circulation in the Earthworm. The red colour indicates arterial, the blue, venous, and the purple, mixed blood. L.I = lateral intestinal vessels.

From the supra-intestinal vessel, which corresponds to the heart of other Invertebrates, the blood passes through the pseudo-hearts and lateral intestinal and œsophageal vessels to the supra-neural. That portion which passes through the pseudo-hearts is arterial blood, but that which reaches the supra-neural vessel from the lateral intestinal and œsophageal, through the sub-intestinal vessel, is rendered venous by passing through the capillaries of the wall of the alimentary canal; thus the blood contained in the supra-neural vessel is a mixture of arterial and venous blood. From this vessel it is carried to the capillaries of the nephridia, by which time it is probably rendered wholly venous, thence it passes to the sub-neural vessel, and from this through the vessels of the body-wall (somatic capillary plexus) to the supra-intestinal again. While traversing the somatic capillary plexus it becomes oxygenated (cp. p. 244).

CHAPTER I

INTRODUCTION

The Scope of Biology.

Biology (*bios*, 'life,' and *logos*, 'discourse' or 'science') is the science that concerns itself with the study of living things in all their manifold variety of structure and manifestation of complicated activities. All that pertains to life, from the phenomena presented by man in his social state, whether in health or disease, to those exhibited by bacteria in the preparation of indigo and the ripening of butter or cheese, or of the animalcule crawling in the mud of its pond, are embraced in the wide range of its field of study.

It is naturally divisible into two great divisions : **Zoology**, or the study of animal life; **Botany**, or the study of plant life. Every organism belonging to either of these two great kingdoms may be studied from two distinct yet very intimately related aspects, for it may be regarded either as a machine at rest, when we confine ourselves to an investigation of its structure, or we may view it as a machine in action and limit ourselves mainly to a study of its activities. The subdivision of Biology which is concerned with the study of structure in its widest meaning is called **Morphology** (*morphē*, 'form,' and *logos*, 'a science'), and that to which is relegated the study of activities or functions, **Physiology**.

Morphology. Studied from the morphological aspect, an organism may be seen by ordinary dissection to be composed of organs or parts, such as muscle, stomach, intestine, brain and heart among animals, or leaf, root, stem and flower among the higher plants. The study of the structure and relation of these constitutes that division of morphology called **Anatomy**, which may, therefore, be defined as the study of gross structure; and while, in the main, it may be pursued

by means of the scalpel and the unaided vision only, in the anatomical study of the smaller animals, such as water-fleas and some of the flat-worms, and the internal structure of the stems, leaves and roots of plants, the aid of optical apparatus to assist the vision is absolutely requisite. Anatomy, thus pursued, reveals the fact, that not only are organisms composed of organs, but that these are in their turn made up of **tissues**, the study of which involves the use of the compound microscope and a very elaborate and refined micro-technique; and to this branch of morphology the name of **Histology** is applied.

Histology, therefore, is the study of tissue, or, as it is sometimes defined, the study of minute structure, and concerns itself with the ultimate analysis of that. The cardinal fact, arising out of histological investigation, is that every adult organism, no matter however complex its organization, is but an aggregate of structural units, called **cells**, which are united together in very various ways, to form tissue. However much these groups of cells (tissues) may differ from one another in the adult organism, either morphologically or physiologically, it is a demonstrated fact that they have all arisen from a mass of cells, structurally and physiologically identical, and which in their turn were derived from a single cell, the **egg** or **ovum**. The process by which this remarkable transformation takes place, i.e. the derivation of highly specialized and complex tissues from a generalized and simple mass of cells, may be spoken of as one of **differentiation**; and since the nature of the changes through which they pass may be either those relating to their activities or to their structure, we may discern between physiological and morphological differentiation respectively. The two processes are, however, so very intimately related, that a morphological differentiation necessarily implies a correlated physiological one.

Arising from the study of the form and relation of the cell as a component element of tissue, the more detailed and exact investigation of the cell as an entity has very naturally resulted; and in comparatively recent years a new branch of morphology, i.e. **Cytology**, has taken origin and is undergoing a very rapid development. The business of cytology is the study of the structure and activities of that which, at the present time, is regarded as the ultimate structural unit of the organism. Considered in its most general aspect, this unit consists of a minute mass of a colloidal substance called **protoplasm**, containing embedded within it a spheroidal mass of denser nature but similar chemical composition, the **nucleus**. In the vegetable kingdom

the structural unit or cell is further composed of a limiting layer surrounding and enclosing the protoplasm of the cell, and called the **cell-wall**; this in its primitive condition has a chemical composition, similar to that of starch, $C_6H_{10}O_5$, but of very different physical characters and reactions. To this material the name of **cellulose** is applied; and since the cell-wall of every vegetable cell is, or was in its original condition, composed of it, cellulose has come to be regarded as one of the most constant and diagnostic substances of the plant kingdom. The animal cell, on the other hand, is devoid of any distinctive cell-wall, and in such cases where one may questionably exist, it is doubtful as to how far it is a distinct membrane or merely a denser layer of the cell substance due to the physical property of surface tension, where the cell surface comes into contact with a medium of different density to that of its own substance. But whether a cell-wall is, or is not, present in the animal cell, it is in no way an essential part of the morphological unit, for there are many cells, vegetable as well as animal, which pass the part or whole of their existence as a naked mass of protoplasm. The same consideration holds equally true of the nucleus, for though it is uniformly present in both plant and animal cells, there are some lowly animals and plants in which its presence has never yet been demonstrated. Nevertheless, when present, there is reason for believing that it is the governing centre of the cell, that it controls and directs the activities which are there proceeding, and it would appear to be in some way intimately connected with the nutrition of the cell substance. It is the essential portion of all male sexual cells, they being, in fact, but little else than nucleus; and though in the female sexual cell there is added an amount of protoplasm which varies with different eggs, and that is often out of all proportion when contrasted in respect of quantity to the nucleus, yet the part which this plays, though important, is altogether secondary and adaptive, and the nucleus is as equally the essential constituent as that in the male cell.

One of the first well-known properties of cells, and perhaps one of the most remarkable, is the power of almost indefinite division and subdivision which they may exhibit under certain conditions. Leaving out of consideration the asexual reproduction of the lower animals and plants and certain exceptional cases, it would appear that the fusion of two elements, i.e. that of the male nucleus with the female nucleus, is necessary to start the inherent but inhibited power of the female cell to divide and subdivide its substance, each portion

growing until it attains the size of the parent cell, when it repeats the same phenomena of division and growth. By the continuation of such processes, which are ultimately provisionally limited, accompanied by a progressive morphological and physiological differentiation of the resulting cellular masses, there is produced a new organism, which repeats the structure and the characteristic features of the parents whence the two sexual cells (gametes) were derived. The transmission of the characters of the parents, through the mother to the offspring, is one of the most prominent facts of biological science, and a real conception of its true nature and significance will doubtless be only gained by very exact experimental cytological investigations.

But as the history of physiology is a record of experimental science preceded by a long period of purely morphological studies, so with respect to all questions relating to the cell. The final causation of heredity, as well as all other abstruse questions relating to the physiology of the cell which are as yet unsolved, will be only finally approached by the experimental method after a greater or longer period of purely morphological studies. And, during the past few years, there have not been wanting evident signs that these cyto-morphological studies are being pushed to deeper issues, and the nature of those internal structural changes of the cell, which are in the main but the gross expression of complicated molecular changes—a 'molecular war dance'—set in action by the external and complicated forces at play upon the cell, is becoming more intimately and accurately known. These changes are in the main connected with the 'kernel' or nucleus of the cell, and since they will be described in detail in the chapter on karyokinesis, we need not here dwell further upon them, other than to emphasize the probability that an accurate and detailed knowledge of such changes will possibly, indeed almost certainly, direct the path of subsequent experimental investigation—a field of inquiry, which when thoroughly explored may lead to results of an exceedingly far-reaching nature.

Embryology. An adult organism has not always been what it is, for however complex its matured organization, it has had a beginning as simple as that of the most simple organism. The beginning of the rabbit and the *Amœba* are the same, but the end is very different; for while the latter does not pass one stage higher than its first, the former passes through a complicated series of developmental changes to a very complex organization. The study of these structural changes up to the period of birth constitutes that division of morpho-

logy known as **embryology**, which may therefore be defined as the study of progressive structure.

No organism arises except as the progeny of another, and in all cases the offspring must be regarded merely as a unicellular bud or germ separated from the parent, which in some cases may develop, by cell division, directly into a new organism, that may or may not resemble its parent; and in others, development does not take place until fusion with another unicellular bud—in most cases differing from it in form—has taken place, and in this case also the immediate offspring may or may not resemble the parent whence it took its origin. But in either instance the ultimate form of progeny resembles the parent or parents, whence were derived the reproductive cell or cells, and the fact that the immediate offspring does not in some cases resemble the parent is due to the interposition in the life cycle of one or more so-called generations (*see below*). The direct development of the reproductive cell without fusion with any other element is known as **agamogenesis** or **asexual reproduction**; and the fusion of two germ cells, prior to development resulting, as **gamogenesis** or **sexual reproduction**. In the latter case the two germ cells are usually distinguishable from one another by very definite characters, and are spoken of as male and female elements or **gametes**, of which the former is usually small and motile, while the latter is much larger and immotile. In several instances, however, the reverse holds good, and in *Hydra* both male (sperm) and female (ova) elements are active. In some cases, which can only provisionally and with doubt be classed with sexual reproductive processes, the two gametes are identical in form, size, and structure, as far as can be ascertained; and to this process the term **conjugation** is applied.

In some organisms the life history is comprised of two distinct phases, consisting of an alternation of agamogenetically developed individuals with those gamogenetically reproduced. Thus A, the asexual individual, produces B agamogenetically, and that developing sexual organs reproduces A gamogenetically, which in its turn again agamogenetically produces B, and so on. This alternation of an asexual with a sexual individual in the life cycle of an organism is spoken of as an 'alternation of generations.' The **agamobium** or asexual generation differs from the **gamobium** or sexual (sexual-organ producing) generation in form, structure, and sometimes even in its degree of organization. It is of very frequent occurrence among

the Hydrozoa, a sub-class to which *Hydra* belongs and the Ascidians, and it is further illustrated among ferns and mosses. In some cases the two generations are perfectly independent of each other, but in others they may be more or less intimately connected.

Embryological facts may be regarded from two aspects, the one having to do with the development of the organism as an individual, and the other considering it in its relation to the race. Every rabbit passes through a series of developmental changes which are the same as those of every other rabbit, and viewed only in the light of its development as an entity, the organism becomes the subject of ontogenetic study. **Ontogeny**, therefore, is the study of the development of any single individual; or since every individual of a species develops in the same manner, exhibiting the same detailed developmental changes, it may be defined as the study of the development of a species. A species, however, does not stand alone, for it is connected by very intimate structural resemblances to other *species*, and the species of one *genus* may be similarly connected with those of another. And when the genera are grouped into assemblages or *Families*, and these into *Classes*, the different Families and Classes, though differing from one another in certain structural characters, are yet related by one or more features common to them all. The comparisons of characters thus made are those of adult organisms; but if these comparisons be made at different stages in the development of the organism, confining ourselves for the moment to Vertebrate development, it is found that the earlier the stage chosen for comparison, the more numerous the resemblances become, and this to such an extent that certain characters which may persist throughout life in one class may, though present in a very pronounced fashion, be purely transitory and confined to one stage of development in another. This is very markedly so in the case of the gill-clefts, which persisting throughout life in fishes, in the majority of Amphibia are present in a functionally active state only in the larval period of development, disappearing altogether in adult life; while in reptiles, birds, and mammals they are present as less well-pronounced structures in the earlier stages of development only.

There can be offered no adequate explanation of the presence of such typically aquatic structures in animals which throughout life breathe by means of lungs, other than that they are vestigial organs derived from some gill-breathing ancestor, and that are now in the course of disappearing in its terrestrial descendants. If this be so,

then an organism in the course of its development throws some light upon its ancestral history; and the study of embryology with a view of elucidating the pedigree of an organism is called **Phyllogeny.**

No better example of the application of ontogenetic and phyllogenetic methods of research can be described than that of the case of the domestic horse (*Equus caballus*). The geological history of this animal has been worked out with a completeness unparalleled elsewhere in the Animal Kingdom, and from the fossil remains of two series; of which one occurs in the Old and the other in the New World, the latter being more complete than the former. The tertiary rocks of America, like those of Europe, are divided into *Pleistocene*, *Pliocene*, *Miocene*, and *Eocene*, of which the last named is the oldest and the first the newest of the series. The horse is represented in the geological deposits of both continents, but for some unknown reason it became extinct in America long before the colonization of that country by Europeans. The first fossil remains of the horse in America are found in the deposits of the *Upper Pliocene*, and they are in no way different from the corresponding portions in the recent horse, which is an animal whose limbs have become modified in accordance with the requirements of rapidity of flight over undulating plains and a firm ground. Both the fore- and hind-limbs of the horse possess only one digit (third finger and toe respectively) and two splint-bones, one on either side of the functional digit, which correspond in position to the bones of the middle hand or foot respectively. In the *Middle Pliocene*, the remains of an animal (*Pliohippus*) slightly smaller than the horse, and possessing its small hooflets, is found; farther down in the *Lower Pliocene*, an animal about as large as the ass, called *Protohippus*, is found, whose fore- and hind-limbs both possess three fingers and toes respectively, but only the middle one is functional and reaches the ground. Earlier still, in the *Upper Miocene*, *Miohippus*, of slightly larger stature than a sheep, is found, whose limbs possess three functionally developed digits and a small splint-bone on the fore-limbs; in the *Lower Miocene*, a smaller animal, *Mesohippus*, has the same three functional digits, but the splint-bone is much larger. In the *Upper Eocene*, *Orohippus* has four digits or toes, of which only three reach the ground, the smaller one corresponding in position to the splint-bone of *Mesohippus*; in the early Eocene, *Eohippus*, with four functional digits and a remnant of a fifth, is found. As we search backwards through the record of the rocks, we can thus trace

the successive stages by which the one-toed and one-fingered horse has been derived from a five-toed and five-fingered ancestor; and a comparison of the horse's limb with those of the animals mentioned above shows that the two splint-bones correspond to the second and fourth digits and the functional toe to the third one of the pentadactyl limb of the horse's ancestor.

In Europe the record, though not quite so complete, is equally convincing. The earliest form is a *Palæotherium*, which possesses three functional toes and is followed later by *Anchitherium*, in which the two side digits no longer reach the ground and the middle one has become larger; this condition is more pronounced in *Hipparion* of the *Middle Tertiary*, an animal which is the European representative of the American *Protohippus*. By the disappearance of the bones of the outer toes, the condition of the horse is attained.

Palæontological facts have thus conclusively shown the line of descent of the horse, as well as demonstrating the nature of the changes by which, step by step, the one-toed animal has been derived from a five-toed predecessor. It has shown us that the marshy surface and disturbed times of the *Eocene* was peopled, among a myriad of other organisms, by animals of the size of our larger dogs, probably slowly moving in their locomotion, and possessing five toes on the hind-limb and five on the fore. Among the tribe of the Eohippi there appeared from time to time animals in which the first toe lost its phalanges, at first perhaps only occasionally, but in the later descendants of these the loss became more constant, until ultimately it became fixed. The loss of this encumbrance doubtless aided the facility with which the animal could move, and those members of the Eohippi which had lost the phalanges of the first toe had a small advantage over those which had not. Among these modified individuals there occasionally arose members in which the splint-bone of the first digit became smaller or was absent, and the suppression of this gradually becoming more constant in its occurrence, there was ultimately produced animals constantly without it, i.e. *Orohippus*. But this modification had not been brought about without cause, and very possibly the physical environment of the times was such that greater fleetness or firmness of foot became more necessary as time progressed, in order to ensure the sufficiently rapid possession of food. Under such circumstances, the unmodified individuals would be less favourably placed than the modified ones, and in time of scarcity of food, arising from whatever cause, they would be those that would die of hunger, and in course

of time become exterminated. At any rate, the extinction is a matter of fact, for *Eohippus* does not occur, and is replaced by *Orohippus* in the *Middle Eocene*; and by similar processes, and in a similar manner, *Orohippus* was followed by *Mesohippus*, this by *Miohippus*, which in its turn was succeeded by *Protohippus*, and this by the equine *Pliohippus*, the series culminating in the horse. Thus, in the remote ancestral tribe of the horse, we see how, by the appearance of what was probably a spontaneous variation, at first inconstant, but becoming with every succeeding generation more marked and constant, new genera and even new families have arisen in the course of immense ages. The student must not imagine that the line of descent is as simple or as direct as he might at first sight conceive, and neither must he gather the impression that the *Eohippus* directly gave rise to the *Orohippus*, and this to the *Mesohippus*. He must remember that the geological record is imperfect, for whole groups of animals have passed away without leaving a single trace of their existence; and indeed, with regard to terrestrial animals such as we are now considering, preservation of their remains is the exception, total decay the rule. Moreover, the pages of the geological record, as they are inscribed in the rocks, have not yet been exhaustively examined, and for these reasons the geological history of the horse, though fairly complete, is not perfect. Only the main features in the retrospect of its eventful and intensely fascinating history have been left, and the minor details are in all probability for ever lost. We know that variations do occur in animals, which at first are casual, then they become more frequent; then they occur as often as not, and ultimately their occurrence becomes the rule, their absence the exception. Thus the small front premolar of *Palæotherium* is smaller still in *Anchitherium*, but still constantly occurs; in the *Hipparion* it is found missing as often as it occurs, and in our present horses it is extremely rare as the 'wolf's tooth,' and in the course of time it will completely disappear.

The series of changes that led to the appearance of the horse may be summed up in the following speculative sketch: The Eocene period, which was peopled among others by the tribe of the Eohippi, was a period of great geological unrest; great land masses were slowly sinking beneath the sea, and some of the great alpine chain of mountains of the present day were being formed beneath the ocean, while others were in the course of elevation above sea-level. These elevations and subsidences were not sudden and cataclysmic, but occupied hundreds of thousands of years; there is evidence to show

that the greater portion of Europe, and a large part of America, were at this period beneath the surface of the sea, or but little above it. The physical conditions of such a period must have been characterized by the presence of extensive marshy swamps, with here and there eminences of dry ground. Under these swampy conditions of the ground, *Eohippus*, with its wide tetradactyl—and the then but recently pentadactyl—hand and foot, was favourably adapted, for it could move, if but slowly, at any rate with security.

In the latter part of the Eocene epoch, the elevation of the ground was still proceeding, and much of it had become drier and firmer; during the same time there had arisen among the Eohippi stock certain individuals in which a spontaneous variation had arisen in the form of a less well-developed fourth toe (*Orohippus*). We know that a spontaneous variation of this sort is hereditarily transmitted, and that if both parents possess it, that the variation in the offspring is accentuated. Now we may imagine, for there is nothing improbable or inconsistent with known facts in so doing, that such a favourable sexual union, or for the matter of that, that several such occurred. There would thus arise a progeny with strong innate and congenital tendency to a reduction of the fourth toe; and this progeny would interbreed and the variation become still more accentuated, until only a splint-bone (metatarsal) of the fourth toe was left. Thus would arise the tribe of Mesohippi. If we suppose that this variation in the direction of the loss of digits conferred any advantage upon the individuals beyond that possessed by those in which such variation had not appeared; that, for instance, in the struggle for existence resulting from the tendency of animals to reproduce beyond the means of subsistence, a three-toed animal could move more quickly than a four-toed one, it would more easily obtain its food and have better chances of surviving and procreating its species than its less favourably adapted fellow.

And this in reality must have happened; for as the land gradually rose higher above the surface of the sea, the swampy areæ favourable to the four-toed Eohippi would become more and more limited and the food supply therefore less, while the dry and firm areæ would correspondingly increase and the food material which it could produce. And those forms which were best adapted to move over firm and dry ground would have more chances of surviving and reproducing their species than those that were only adapted for marshy swamps. And in connexion with this greater rapidity of motion, it must be remem-

bered that the loss of the toes was correlated with increase in the length of the limbs, in size of body, and alteration of the pattern of the teeth. All the swiftly moving ungulate animals of to-day are either single-toed like the horse, or double-toed like the deer; and for mechanical purposes, the double-toed forms are really single-toed, for the two metacarpals of the fore-limb and metatarsals of the hind-limb are fused together in most instances.

Just as the three-toed tribe arose from the four-toed one, by a 'sport' or variation, so too did the one-toed tribe arise from the three-toed one; and by processes identical to those which established permanently the sport that gave rise to the three-toed tribe, the one-toed tribe became established. And we may suppose that the correlated increase of limb, and body, and modification of the teeth, enabled this latter form to be better adapted to the conditions of the times in which it lived, so that while it lived and flourished, the former gradually became exterminated.

Thus we may say that the horse has been evolved, by Nature selecting those forms which had arisen from pre-existing ones by the variation of some organ; this variation conferred some advantage on the animal possessing it, so that in the struggle for existence—in all probability as keen then as now, since the laws of Nature as we know them are continuous and eternal—it was better adapted to find its food.

This theory, explaining how one form of animal arises from a pre-existing one, and why some forms persist, while others closely allied become extinct, is known as that of **Natural Selection**, and was simultaneously announced by Darwin and Wallace.

Geological investigation has shown that the physical features of any given area of the Earth's surface has changed from time to time; so that that which was once covered with a tropical vegetation is now covered with an ice-sheet, and may in some remote future again become clothed with the thick mantle of tropical growth. These changes occupy immense periods of time, and adopting a very rough and doubtful approximation, we may say that from the Palæotheridæ (probable common ancestry of our odd-hoofed ungulates) to the present represents something like thirty million years. As the physical conditions changed, those members of the old group of animals which did not vary, or whose structural variations did not adapt them to the changing conditions, became eliminated in the course of time, and were replaced by those forms whose variations had adapted them to their new physical environment.

Thus, apart from any theoretical explanation as to how or why certain changes have taken place, we learn from the facts of palæontology that a succession of forms can be traced, commencing with the four-toed Eohippus, in which by a gradual reduction of the number of digits, the one-toed and one-fingered horse is reached. And from these facts, together with the one that the four-toed forms preceded in geological time the three-toed forms, and these the one-toed forms, we come to the conclusion that the ancestors of the horse have successively passed through these stages.

And if this is so, and an animal in the course of its ontogeny repeats, in an abbreviated form, the chief stages of its ancestral evolution, we should expect that in the development of the horse's limb, some traces of the lost digits would be found. And, as a matter of fact, such is the case, for nodules of cartilage—it must be remembered that bone is preceded by cartilage—appear in the foot, which occupy the position of some of the lost phalanges; they are only transitory and soon disappear.

Moreover, if the horse has been derived from an ancestral stock that possessed more digits, and if heredity is strong and potent, does it ever happen that a horse 'harps back' to an ancestral condition, and exhibits three or more functionally developed toes, or other ancestral features? To such a question we must reply in the affirmative, for horses have been met with that possessed more than one toe, which had feet that were veritable Hipparion feet, in that the two splint-bones had their corresponding digits, and the so-called 'chestnuts'[1] on all four limbs. Occasionally the horse's jaw will develop a tooth (the wolf's tooth) in front of the premolars, which has no place in the normal dentition of the animal, but constantly occurs in *Anchitherium* and as often as not in *Hipparion*. These variations are not 'monstrosities,' but merely the occasional appearance of a structure that was once a normal and constant feature in the ancestor of the animal, which is now in the course of disappearing. Such structures are not uncommon throughout the Animal Kingdom, and are known under the name of **vestigial structures**, and must be clearly distinguished from structural variations that are indicative of progression, i.e. that have yet to attain their maximum development, and are **rudimentary structures**.

The appearance in an organism of a structure that is not normally

[1] The 'chestnuts' are horny warts, which probably correspond to the hoof of the thumb and great toe.

present, and which may be reasonably interpreted as being an ancestral vestige, is called **atavism**. So that the wolf's tooth and the Hipparion feet of the horse are atavistic structures.

The comparison between the palæontological facts of the horse's evolution, and its ontogeny, backed by the phenomena of atavism, supports the conclusion that the development of an animal is a recapitulation of its ancestral evolution; so that we are justified in saying, that in general, ontogeny is summarized phyllogeny. There are, however, certain very remarkable developmental phenomena among insects and echinodermata, that forbid any such conclusion being applied to them. In some members of the latter class for instance, the greater portion of the organism which arises from the egg disappears; the permanent organism arises within that shortly before its disappearance, and is but an exceedingly small portion of the whole. This cannot be looked upon as indicating an ancestral evolution, for however much an organism may desire to do so, it cannot throw off its ancestry, nor follow independently two lines of evolution; that is a feat which even man, blinded by prejudice and exalted by a vain sense of superiority, has not been able to do. And there is good reason for believing that many embryonic stages, like the later permanent one, are largely adaptive to peculiar conditions.

Homology and Analogy. In popular acceptation it is vaguely thought that the wings of an insect and a bird are similar things, and that the fore-legs of a donkey and the wings of a sparrow have nothing in common. But, apart from the fact that both serve as organs of aërial propulsion, there is no resemblance, anatomically or developmentally, between the wings of insects and birds. In the latter, the wing is essentially of mesoblastic origin, its muscles, blood-vessels, and skeletal structures all arising from that germinal layer; while in the insect the wings are merely chitinous plates of epiblastic origin, and of simple anatomical structure. Thus, though they function in a similar manner, they differ fundamentally in their embryological origin and their anatomy; organs which are physiologically similar but morphologically different are called **analogous organs**. On the other hand, the fore-legs of a donkey, or any other mammal, and the wings of a sparrow, or other bird, arise in fundamentally the same way and from the same germinal layer, and are anatomically fashioned alike; and they are used for the same physiological purpose, i.e. that of locomotion. The fore-limbs of man are embryologically and anatomically very similar to those of the rabbit, but he does not

use them for locomotion, for they are to a large extent organs of prehension, and of sense and associated powers of delicate manipulation. Organs which are thus morphologically alike, and may or may not be physiologically similar, are called **homologous organs.**

Thus the trunk of an elephant is homologous to the nose of other mammals, and its tusks to their incisors. The mouth parts (jaws and maxillæ) of an insect are homologous with its legs, and the swimmerets of a crayfish with its great chela or tearing organ; the teeth of fishes are homologous with the scales embedded in their skin, and the nasal ‘horns’ of rhinoceroses with the hair of other mammals. The gills of the fresh-water mussel, crayfish and dogfish are analogous but not homologous, since they perform the same physiological functions; but in Vertebrates, the gills are outgrowths of the gut and hypoblastic in origin, while in the mussel and crayfish they are outgrowths of the body-wall and epiblastic in origin.

Homoplasy. Very often there may be found in animals which have no close genetic relationship organs of similar form. The similarity in these instances is probably to be explained by the evolution of ancestrally distinct forms under similar environmental conditions. That is, that two forms, having no genetic relationship and maybe widely separated geographically, evolve under similar physical conditions, and therefore along structurally parallel lines. Among sponges for instance, it is probable that the different groups may have had independent origins, but owing to the fact that certain members of different groups have been acted upon during the course of their evolution by a similar environment, their canal systems are similar also.

Physiology. An organism studied in its entirety is a machine in motion. It is a structure moved to action by the play of certain forces—an organization whose minutest fabric is the seat of molecular agitation. The study of these forces and of the activities which are the visible expressions of their application, belongs to the domain of **Physiology.** In the earlier periods of physiological inquiry, the dominant idea that guided every research was that the nature of the activity depended upon the structure, i.e. given a certain organ and it would perform a definite action or function. Such an idea, though apparently obvious, is yet probably, in part at least, a transposition of cause and effect, for the form and structure of the organ is not the immediate cause of its activities, but rather the effect; in other words, it is rather the nature of the forces at play which

determine the structure of an organ, and not the nature of the structure that prescribes the activity. The beating heart of a three-day chick is actively contractile, but it contains not a trace of muscle fibre; the structure is absent but the activity is present. The physiological differentiation has preceded the morphological, and the latter will arise in response to the stimulus of the former; contraction is here the outcome of the hidden forces at work, and the subsequent muscular differentiation is a structural adaptation to the requirements of those. The ultimate aim of physiology is to unravel the complicated skein of those molecular changes which constitute life—which are coincident with life and cease with its cessation. The more complicated and highly organized the organism, the more subtle and complex the 'molecular war dance' that is the seat of its activities; and consequently the fundamental facts of physiology are best studied in the simpler organisms, where the 'dance of the molecules,' though still complicated, is simple compared with that of the higher organisms.

A knowledge of the physiology of the unicellular *Amœba* reveals the fact that it is capable of manifesting all the activities of the higher organisms, the phenomena of mind being excluded, and yet it is but a microscopic particle of a colloidal, semi-fluid substance, called **protoplasm.** It is, therefore, obvious that though the very complex organization of man and the higher animals is a requisite possession for the performance of their higher functions, it is in no wise necessary for the manifestation of life itself. Further, this substance protoplasm is always found in association with life, and apart from it there has been no life, so that we may look upon it as the material, which receiving certain forces from sources that we have yet to study, converts them into the phenomena of life. It is therefore, in the words of the late Professor Huxley, the 'physical basis of life'—the substance which receiving the imprint of the molecular dance of external forces converts them into the molecular dance of life.

Protoplasm, therefore, is a substance alike of great importance and extreme interest, and it is necessary that the student should acquire some clear idea of its nature. In the earlier years of its discovery, it was thought that the protoplasm of plants and animals was different, but to-day it is known to be fundamentally the same among the organisms of the two great classes of the living kingdom. It may be seen most favourably in the Proteus Animalcule (*Amœba*), in the stinging hairs of the nettle, in the cells of *Chara* (Stonewort) and *Elodea* (Canadian Water Weed), and in the white corpuscles (leucocytes)

of the blood of animals. It consists of a transparent, colourless, sometimes hyaline, sometimes granular material, with a refractive index higher than that of water. In consistency it is often described as semi-fluid, but it may more correctly be called viscous, the degree of its viscosity depending upon the amount of water held within its substance. In living organisms like *Amœba* it can be generally discerned to consist of an inner granular portion, the **endoplasm**, surrounded by an outer perfectly clear portion, the **ectoplasm**. The granules contained in the endoplasm are of different sizes, and to the larger ones, which are regarded themselves as being organic units and capable of independent assimilation and reproduction, the name of **bioplasts** or **microsomes** has been applied. Doubtless some of the granules represent stores of reserve food material, while others may represent waste products in the course of elimination. Examined with the higher powers of the microscope, protoplasm presents a reticular appearance which varies with different protoplasms, and which has been interpreted in one of two ways. One view is that protoplasm consists of a reticulum composed of a denser substance, the **spongioplasm**, the meshes of which are filled with a softer, more liquid substance, the **hyaloplasm**. A modification of this view regards it as being composed of separate fibrils of denser substance interlacing in a less dense substance. This is known as the **fibrillar theory** of protoplasm, and differs from the **reticular theory**, in that while the latter considers the threads of the meshwork as being composed of a continuous net, the former regards it as consisting of a number of separate fibres interwoven. The other view regards it as being composed of alveoli, i. e. having a honeycombed structure, the walls or limits of the alveoli consisting of a denser, and the contents of a less dense material. Butschli, by grinding up $NaCO_3$ in thickened olive oil and placing one drop in water, obtained a saponified mass, the appearance of which is remarkably like that of living protoplasm; it has an alveolar structure, in which the limiting layer of the alveoli consists of oil and the contents of a solution of $NaCO_3$ in water. Such a preparation not only exhibits a protoplasm-like structure, but it imitates the amœboid movements which are characteristic of a large number of unicellular organisms. In this experiment the flowing movements are no doubt due to surface tensions, and it is a question as yet unsolved, as to how far the movements of living protoplasm are due, wholly or in part, to the same cause.

The chemical composition of protoplasm has not yet been accurately

ascertained, for the methods employed in chemical analysis result in its death, and it is doubtful whether the composition of dead and living protoplasm is quite the same. As far as our knowledge goes, protoplasm may be regarded as a more or less complicated mixture of unstable phosphorus containing nitrogenous compounds, known as **proteids**, of which white of egg (albumin) is a good representative.

Chemically considered, the percentage composition of proteids may be taken as approximating to the following: **Carbon**, 51· to 54·; **Hydrogen**, 6·5 to 7·; **Nitrogen**, 15 to 17; **Oxygen**, 20·9 to 23·5; **Sulphur**, ·3 to 2·0; **Phosphorus**, in traces. They are recognizable by certain reactions, of which the following are those more usually employed: (1) When boiled with nitric acid they turn yellow, and upon cooling and adding ammonia the yellow is deepened into orange. (2) When excess of potassium hydrate and a drop of copper sulphate are added to them, they give a purple colouration. (3) With Millon's reagent (mixed nitrate and nitrate of mercury) they give a white or pinkish precipitate, becoming more pink on boiling.

Physically considered, they are all amorphous and non-crystallizable, so that they possess no power of filtering through either animal or vegetable membranes, and are hence called **colloidal** substances to distinguish them from substances which can, or **crystalloids**. All proteids undergo heat stiffening or coagulation, the exact temperature of which varies for different proteids, but may be said to range from 55° C. to 75° C. for the class; and in so doing they become insoluble in their usual media, i. e. water, or dilute or concentrated saline solutions, and are only soluble in strong acids or alkalis, undergoing chemical disintegration in the process.

Living protoplasm is a very different substance from dead protoplasm, for the latter if left to itself will undergo gradual decay and waste away until nothing is left. In so doing it will evolve heat, carbon dioxide, ammonia, water, and small quantities of other bodies, all of which represent the final stage in a process of oxidation—the splitting up of the complex protoplasm into more highly oxidized and much simpler substances. Living protoplasm on the other hand, while evolving all these substances, replacing ammonia wholly or in part by other nitrogenous compounds, not only wastes away, but undergoes a concurrent reintegration or repair; so that while at no two consecutive moments it is chemically the same, it nevertheless remains, so long as the organism lives, as a substance whose bulk

does not diminish but rather may increase. Living protoplasm, therefore, represents the mean between these two processes of disintegration and reintegration, and so long as they are equally active growth remains stationary ; while if the latter process is greater than the former, the protoplasm increases in bulk or grows, and it declines or wastes from the moment that the processes of decay are predominant over those of repair.

The growth of living protoplasm is very different from that of such a body as a crystal, for whereas the latter, if submerged in a solution of its own substance, will grow by the addition of successive layers to those already existing—a process of growth which is known as **accretion**—the former grows only by the intercalation of new molecules between those previously existing in the substance of the protoplasm, or by a process of **intersusception.** It further differs in that the material thus intercalated reaches the condition of living protoplasm only as the result of a long series of constructive changes, whereas that laid down upon the surface of a crystal remains unaltered throughout the whole process.

The material that is ultimately destined to form new protoplasm may be of very diverse nature, and is included under the general term of 'food'; but whatever its nature, whether it is the gaseous or liquid food of green plants, or the more elaborate food of fungi and animals, it is destined to pass, step by step, through an ascending series of changes, at each step in which it becomes more complex, less like food and more like living protoplasm ; at the top step in the series, it becomes actual living protoplasm, and reaches the zenith of its complexity. Thenceforth it passes down the descending series, at each step of which it becomes simpler in composition, less like protoplasm, and more like the waste products towards which it is hastening, and which represent the final stage in its downward path. The chemical and physical processes involved in the building up and breaking down of protoplasm, are designated in a general sense by the term **metabolism** ; while those which are involved in the sole act of construction are included in that of **anabolism**, and those which are concerned only with the destructive changes, are indicated by that of **katabolism.** The processes which are involved in the gradual conversion of food into living protoplasm may be spoken of as those of **assimilation**, so that we may speak of assimilative metabolism, instead of anabolism, or of destructive metabolism instead of katabolism.

Anabolism and katabolism, therefore, represent certain processes

which are going on within living protoplasm; but these processes are connected with changes in material, and although we know but little of the intermediate stages which exist between food at the beginning and of waste products at the end of metabolism, we speak of the various materials that arise during anabolism as **anastates** and of those produced during katabolism as **katastates**.

The whole processes of metabolism are intimately associated with those of respiration, and so long as an organism lives it must respire, that is, take in a supply of oxygen, which entering into composition with living protoplasm, starts those series of destructive oxidative processes which we have already spoken of as katabolism; and inasmuch as oxygen thus becomes a necessary element of metabolism it is a true food. We have seen that assimilation ends when the crude food material has become part of the living protoplasm, so that katabolism begins with the advent of oxidation. Respiration therefore commences where assimilation ends—in the circle of life's activities the one becomes the supplement of the other—and so long as these two processes are proceeding, the protoplasm is a living substance and will so remain. The life of an organism is thus comprised within these two series of processes, and so far as the individual is concerned, there are no others. If, however, the race is to exist and spread, some process by which individuals may increase and multiply must be called into play, and under whatever guise it may present itself, whether of primitive simplicity or elaborated complexity, it is spoken of as **reproduction**.

Reproduction, therefore, has to do with the propagation of the race, and the essential nature of the process may be best understood by an appeal to it under its simplest conditions. The *Amœba* is a minute naked mass of protoplasm, lodging within its substance a kernel or nucleus; by assimilation it grows, and were this to remain unchecked, the growth of the individual and the limits of its size would be endless. And while, perhaps, we may in a certain sense regard growth in the race of *Amœbæ* as eternal, yet growth as far as the individual is concerned is sharply circumscribed, for when an individual reaches the limit of its growth, it constricts itself into two portions, each of which attains the size of the parent whence they were derived. By a repetition of the process, eight *Amœbæ* will be produced from these four, and so on *ad infinitum*. It would thus appear that the phenomena of reproduction, as they are exemplified in their simplest conditions, are manifested by processes which, while preventing the overgrowth

of the organism as an individual, ensure the ever increasing growth of the organism as a race.

Protoplasm is, therefore, a complex substance capable of performing in even its simplest condition all the fundamental requirements of life; and we have said that the phenomena of life are but the visible expressions of constant molecular unrest produced in a 'physical basis' (protoplasm) by the play upon it of external forces. If this be so, it next becomes our first duty to ascertain the source and nature of these forces.

The chemist and physicist have shown us that the phenomena of nature are referable to the existence of certain physical forces, such as light, heat, sound, electricity and magnetism, and to chemical interactions, acting upon matter; and if these are the forces of nature apart from life, we naturally inquire how far they are also the forces of life itself. The quest becomes still more interesting when we recall to mind the greatest generalization of physical science, begotten and developed within the last half-century, i. e. the evolution of physical forces, or the doctrine of the conservation of energy. Heat may be converted into motion or electricity, and electricity and motion into heat; sound and motion may similarly be converted into chemical reaction, and since chemical reaction is but a particular form and combination of physical forces acting upon matter, sound and motion may therefore be converted into the physical forces which are the factors of the chemical reaction. If the physical forces of nature are thus mutually interchangeable, may it not be possible that they are also convertible into those of life? And, conversely, those of life into those of heat, sound, electricity and motion?

To pursue investigations dealing with such problems, it becomes imperative to deal with life in its simplest manifestations and therefore with its simplest organisms; for higher in the scale of life, there are so many interfering factors, that the elimination of all other than the one required, which is a *sine qua non* of an experiment, becomes impossible. The simplest organisms are those which throughout life remain as a single cell—a mere speck of 'physical basis' exhibiting the phenomena of life under its simplest known conditions. It is with such as these that the great problem of life, and perhaps of disease, will ultimately be solved, and with which we here propose to introduce the student to the elementary facts of physiology.

Of the physical forces that play upon living organisms, that which has been the longest and most exhaustively studied is heat,

and we shall commence with considering the effect of varying temperature.

Life is only possible between certain limits of temperature, which varies for different organisms, and in general the more highly organized the organism the smaller is the limit between the minimum and maximum temperature at which it may manifest signs of life; but for all organisms there is a temperature between these two extremes at which all the processes go on most vigorously, and this is the **optimum temperature.** As the temperature rises above this to the **maximum**, or falls below it to the **minimum**, the vital activities begin to diminish and ultimately cease when either extreme is reached; but the cessation of activity is not death, for it is a condition which lasts only as long as the unfavourable temperature, and life will re-manifest itself when a favourable temperature returns; the point of death, however, is but a few degrees below or above the minimum or maximum.

The extremes of temperature vary not only for different organisms, but for the same species under different conditions, for an organism suddenly subjected to a high temperature will be killed at a lower degree than another organism of the same species which has been gradually accustomed to it. Also it would appear that a lower temperature long continued acts like a higher temperature operating over a brief interval of time.

The **ultramaximum temperature**, or death point, of a unicellular organism like *Amœba* is from 40° to 45° C. and its ultraminimum is 0° C.; that of bacteria is 45° C. and their minimum has been lowered to −10° C. and for some time sinking to −18° C., without death resulting; that of yeast, under moist conditions is 53° C. and −5° C. respectively, but in the dry state it may be reduced to the extremely low temperature of solid carbonic acid (−60° C.) without being killed. The spores of many fungi when dry may be subjected to the extremely high temperature of 120° to 125° C., viz. 20° to 25° above the boiling point of water, and yet germination will ensue upon the return of favourable conditions; but the adult plants are killed at a much lower temperature.

The effect of heat upon the growth of organisms offers a certain similarity to that of its effect upon their vital phenomena as a whole, for the same three critical points exist, viz. a minimum temperature, below which growth ceases; an optimum, at which it most rapidly progresses; and a maximum, above which it ceases. Between its

optimum and the average temperature to which the organism is normally subjected in nature, there appears to be a certain relation, for in the case of certain bacilli living under natural conditions at a low temperature their optimum is low, and in the case of others whose normal environmental temperature is high, the optimum is high.

The direction towards which living organisms will trend is also determined to some extent by temperature, for the unicellular *Paramœcia* placed in a trough of water of a different temperature at either end, and which is capable of being varied, will remain uniformly scattered throughout the water when the temperature is about 20° C.; but when the temperature of one end is raised to 38° C. and the other to 26° C., they will aggregate towards the latter and entirely desert the former. Similarly, when one end is reduced to 10° C. and the other is raised to 25° C. they will crowd together at the latter and retreat completely from the former. To this phenomenon the term **thermotaxis** is applied.

No less important than the thermal environment upon the cell, or the organism, is that of light. The growth of the spores of the mushroom and those of the potato-fungus are retarded by light, while the germination of the seeds of the higher plants takes place more quickly if they are subjected to darkness. Very familiar is the difference between the elongated, very tall and yellowish seedling of the mustard plant grown in darkness, and that of the shorter and green one when grown in light. With aquatie plants and tadpoles, on the other hand, diffused daylight appears to favour growth. It is nevertheless a noteworthy fact, that embryonic tissue is usually sheltered from sunlight, for in mammals the embryo is hidden in the maternal body; in birds and reptiles it is invested by a more or less opaque shell and the eggs are usually deposited in dark places; while the eggs of most Amphibia are deeply pigmented with a blaek pigment whieh absorbs the rays of light. Light influenees the direction which an organism will assume, as well as its growth, for zoospores of *Protococcus* placed in a vessel of water, one end of which is directed towards diffused light and the other towards darkness or less intense light, will move towards the former. If, on the other hand, one end be plaeed towards the direct rays of the sun and the other towards darkness, they will retreat from the bright rays and aggregate towards the dark side; they ean thus apparently discriminate between light of different intensities. The phenomena presented by organisms moving towards a region of greater or less intensity of light are known as

photopathy and must be clearly distinguished from the phenomena presented by organisms moving in the direction of the light rays or **phototaxis**. The latter have been clearly demonstrated by certain crucial experiments on unicellular organisms and on certain Metazoans, which were placed under such conditions, that in one instance the field was marked by bands of varying intensities of light but the direction was the same throughout, and in the other the direction of the light was from the side of less intensity. In the first instance the organisms remained uniformly scattered and showed no tendency to aggregate more towards one band of intensity than another ; while in the second instance they all migrated towards the less intensely lighted side, viz. towards the side from which the rays of light proceeded. These organisms, therefore, are not photopathic, but phototactic ; but there are some (*Daphnia*) which are both, viz. influenced alike by the intensity and the direction of the rays of light.

Equally remarkable are the effects of electricity upon living protoplasm, for if a unicellular ciliate organism like *Actinosphærium* be subjected to the influence of the constant current, the effect will depend upon the strength of the current. A weak current causes a retraction of the filamentous pseudopodia lying in the axis of the current, and if it be increased in strength or long continued, the pseudopodia become varicose and break up into droplets ; finally, the protoplasm upon the anode side begins to disintegrate ; and this may ultimately proceed so far as to result in the complete destruction of the animal. If an *Amœba* in a drop of water be subjected to a weak constant current, strong enough to produce contraction but not disintegration, it will retract its pseudopodia on the side directed towards the anode, while those directed towards the kathode remain active, and the organism will in consequence travel towards that, and therefore in a direction away from the contracted side. If *Paramœcia* be placed in a drop of water, at either end of which are the two electrodes, and the current is not too strong, they will migrate towards the kathode or negative electrode. There is thus exhibited by these two unicellular organisms the phenomenon of **electrotaxis**, or the determination of the direction of their locomotion by electrical influences.

Organisms are influenced by the chemical properties of certain substances, for it has been shown that if certain algal plants, which give off oxygen in the light but not in the dark, be placed in water containing certain bacteria (which are practically the simplest known kind of cell), that these will be uniformly dispersed in the water if the whole

be placed in darkness, but that in two minutes after the algal plant has been illuminated and commenced to give off oxygen, a migration of the bacteria towards the plant takes place, and in a very short time they are closely aggregated round it. Upon the light being cut off they commence to migrate outwards and become uniformly scattered in the liquid. In this instance, oxygen appears to exercise an attractive influence upon the bacterial cells, and to determine the direction which they shall take. This substance, however, is not the only one that exercises such an influence, for if bacteria derived from decomposing peas be placed in water, at one end of which is a capillary tube closed at one extremity and containing a weak solution of potassium nitrate, it will be found that they not only aggregate round the open orifice of the tube, but actually enter it, apparently in an endeavour to reach the most potent portion of the attracting substance. In a similar way malic acid determines the direction of the spermatozoids of the Fern-plant; but under normal conditions only within certain limits, for a solution weaker than 0·001 % or stronger than 10 % fails to attract. It is also now a well-established fact, that if a small and very short capillary tube containing formalin be injected beneath the skin of an animal, its presence at once attracts an enormous crowd of the leucocytes (unicellular corpuscles) of the blood, which completely encircle it. Very strange, however, is the fact that there exists no relation between the properties of the attracting substance and any advantage which it may confer upon the attracted cell, for it has been shown that substances like glycerine, which has a nutritive value for bacteria, may be wholly neutral, so far as its attractive influence upon the organism is concerned; while substances like weak solutions of sodium salicylate and morphine, which are fatal poisons, may attract. On the other hand, there are many lowly organisms and zoospores of some of the algæ which are attracted by substances such as oxygen, phosphates, meat extract, &c., which can, and very probably do, offer them supplies of nourishment. The phenomena above described, which may be briefly stated to be those of the effect of chemical substances in determining the direction of living organisms and cells, are comprised under the term of **chemotaxis**.

The phenomena expressed by the term **geotaxis**, or the determination of direction through the influence of gravity, are no less remarkable and significant. If a large number of *Euglenæ* (a unicellular organism) be placed in water, or in moist sand, and constantly shaken up with it, they will constantly rise to the surface, and this after all

disturbing chemotaxic and phototactic influences have been removed. *Paramœcium* responds in a similar manner to the influence of gravity, for if it be placed in a capillary tube of about 20 cm. long, which is held vertically, it will, so long as thermal, chemical, and other influences are not at work, constantly rise to the top; while certain bacteria placed in with it will as constantly sink to the bottom. *Paramœcium* is therefore **negatively geotactic**, viz. moves in a direction opposite to that in which gravity pulls, while certain bacteria are **positively geotactic**, viz. move in the direction in which the force is pulling.

The phenomena presented under the influence of molar agents in determining the direction of certain lowly organisms, and expressed under the name of **thigmotaxis**, are of a highly interesting nature. As in geotaxis and other phenomena relating to direction in response to external stimuli, thigmotaxis may be either positive or negative in nature. *Amœba* is a unicellular organism which exhibits both phases, for if the blunt processes called pseudopodia (Fig. 86) which it normally protrudes be irritated by sudden or somewhat violent contact with a sudden body it will withdraw them; and if the irritation is continually applied upon the same side, that side will remain contracted and locomotion in a direction away from the source of stimulus (**negative thigmotaxis**) will result. On the other hand, an *Amœba* descending in a drop of water will first touch the solid surface by one of its protruded pseudopodia, which will immediately begin to elongate and become affixed to the surface, and as new pseudopodia are thrown out, affixation taking place in each case, the whole organism soon becomes adherent to the surface of the solid, along which it crawls by elongation of its pseudopodia with continual affixation. In this case the organism moves towards the solid surface (**positive thigmotaxis**). *Paramœcia* exhibit the same phenomena in another way, for if certain solid particles are floating in the water in which they are living, they will tend to aggregate around them; and if a spherical grain be placed in a drop of water in which the spermatozoa of the cockroach or the frog are contained, they will aggregate around it. Or, if the spermatozoa of either of these two animals be placed in a drop of water, between a slide and cover slip, they will separate into two layers, a lower attached to the surface of the slide, and an upper attached to the under surface of the cover slip, the water between the two layers being almost devoid of them, or containing only the weak or dying forms.

Living protoplasm contains a considerable quantity of water which varies for different organisms; in some *medusæ* (jelly-fish) it is as high as 95 %, and in some dry seeds it may be below 15 %, while in the majority of living organisms it varies between 60 % and 90 %. Water, therefore, forms a predominant portion of living structures, and it becomes a matter of some importance to ascertain to what extent it may be withdrawn from such without death resulting. It is now a well-established fact that *Paramœcia* may be dried to such an extent as to approach complete desiccation, and to remain in this condition for some considerable time, months or even years, during which period all the processes of life are totally arrested, and upon the subsequent access of moisture, revivification results. Many wheel animalcules (rotifers), which are multicellular organisms of comparatively fairly complex organization, may be dried by the evaporation of the drop of water in which they are living, and kept thus for an hour or more, and will gradually reassume their form and activities upon the access of water. But it is important to note that if the drying be done on a clean slide, death and not merely suspension of life results. It is only when there are sand particles present among which the rotifers may embed themselves, that they can be dried to this extent without death intervening; and this fact throws considerable doubt upon the assumption of some observers that complete desiccation had been attained in their experiments. In nature, many of the unicellular organisms are subjected to periods of drought, during which the water in which they are living completely dries up; and it has been observed that under these conditions the organism assumes a spheroidal shape and encysts itself in a delicate pellicle secreted by its own substance, within which it remains until the return of more favourable conditions. Obviously this is a reaction in response to external stimuli and very probably has to do with preventing the complete drying of the organism. Moreover, many structures, like some of the spores of plants, which can live and retain the power of germination for a prolonged period in air devoid of a trace of moisture, are protected by a thick outer covering. Such facts as these prove very conclusively that complete desiccation is incompatible with the existence of either actual or potential life, and while organisms may live, though with arrested activities, under conditions of almost extreme dryness, yet the complete withdrawal of water from living protoplasm results in inevitable death. For, if it were otherwise, why should animals protect themselves by encystment?

The facts enumerated under the various heads of phototaxis, chemotaxis, geotaxis, thigmotaxis, electrotaxis and desiccation, serve to demonstrate how profound and important is the influence of the purely external chemical and physical environment upon the organism, which in the majority of instances chosen, has purposely been confined to morphological and physiological units or single cells. In fact, the tendency of all modern investigation serves to show that the phenomena of life, at present considered apart from mind, are but highly specialized and exceedingly complicated expressions of purely physical and chemical changes, masked and modified by the peculiar nature of the substance upon which they play.

CHAPTER II

THE CHARACTERS OF THE GREAT DIVISIONS OF THE ANIMAL KINGDOM

THE diversity of structure presented by the Animal Kingdom is at first sight so immense that it is an apparently hopeless task to endeavour to reduce it to order. Careful comparison, however, reveals the fact that all known forms of animal life may be referred to one of two great divisions, viz. the **Protozoa** or the **Metazoa**. The former includes all those animals which remain throughout life in the condition of single cells, and which never advance beyond the stage of morphological and physiological units. It is true that some of these unicellular organisms are more complex than others, but their complexity is due to chemical and physical differences in localized parts of the protoplasm of the cell, and not to structural differentiation. In some cases (*Labyrinthulidea*) a colony is formed by the aggregation of a large number of Protozoa, and in other instances (*Protomyxa*) the single cells become coalesced in a jelly-like mass, called a **plasmodium**, in which the individual form of each cell is lost, so that the colony appears to be composed of a mass of protoplasm with a large number of nuclei scattered through it. But in neither case is there a differentiation into two or more tissues, for so long as the colony exists it remains a homogeneous assemblage, and in the latter case (*Protomyxa*) the compound condition is not permanent.

The **Metazoa** includes all those animals whose organization is

characterized by the possession of two or more definite tissues, which have arisen from the egg by a process of differentiation. The simplest known form of metazöon is virtually a double-layered sac, the opening of which plays the part both of a mouth and an anus, and that leads to a gastric cavity in which digestion takes place. Such a form is well represented by *Hydra*, and is represented in Fig. 83, A. The highest form of metazoön represented by the Mammalia, of which the rabbit may be taken as a type, presents a considerable advance upon this simple organization, inasmuch that in addition to the mouth there is another aperture or anus at the other extremity of the digestive canal, and that between the outer (ectoderm) and inner (endoderm) layers of the body there is developed a cavity which is bounded by a layer unrepresented as such in *Hydra*. The presence of this cavity results from the formation of a third layer, which at a very early period in its development splits into two layers, one of which becomes applied to that (endoderm) lining the digestive canal (enteron), and the other to that (ectoderm) limiting the body externally, thus leaving a cavity between them.

Throughout the Animal Kingdom, the innermost of the three layers is called the **endoderm**, the outermost the **ectoderm**, and the middle the **mesoderm** ; while the cavity which results from the splitting of the latter is called the **cœlom** or **body cavity**.

Among the Metazoa, therefore, we may distinguish between those animals which, like *Hydra*, do not possess a cœlom, as the **Acœlomata**, and those which do, like the earthworm, crayfish, mussel, *Amphioxus*, dogfish, frog, and rabbit, or the **Cœlomata**.

The Metazoa may be otherwise separated into two great groups : the one including all the animals that possess a backbone, the **Vertebrata**, and the other, those which have no dorsal-supporting column, the **Invertebrata**. These two groups, however, are not separated from one another by any rigid limits, for on the one hand, at the top of the Invertebrate scale we find a worm-like animal, called *Balanoglossus*, which possesses a rudimentary backbone and a dorsally situated nerve cord in addition to the characteristically Invertebrate ventral one. On the other hand, at the bottom of the Vertebrate scale, there are placed a group of animals called *Tunicates* or *Sea-Squirts*, the majority of which possess a backbone only during the earlier period of their existence, while in some few (*Appendicularia*) it is retained throughout life. But with these, and a few other exceptions, all Invertebrata are distinguished by the absence of a

backbone (vertebral column, or its precursor, the notochord), and when present, by the ventrally (front) situated nerve cord and the dorsally (back) situated heart. All Vertebrata possess a backbone, either, as in *Amphioxus* and the lamprey, as a cartilaginous rod or *notochord*, or as a vertebral column, composed of distinct pieces (vertebræ) which may remain cartilaginous throughout life or later become ossified (replaced by bone); the heart is always situated in front (ventrally) of the alimentary canal and the nerve cord dorsally. A longitudinal section through the body of a cœlomate Invertebrate will show that it is constructed externally of a limiting body-wall, composed of an outer skin supported by a membrane, and of an internal muscular mass, the body muscles. At the forward (anterior) and hinder (posterior) ends of the body the skin is invaginated to form respectively the mouth and anus, the two terminal apertures being connected by a tube (the alimentary canal) running the whole length of the body. Situated along the back (dorsally) of this is another tube, the heart, which may be variously modified in different animals, but which always receives the blood brought back from all parts of the body. Ventrally to the alimentary canal there is a solid and paired cord which arises anteriorly to the mouth and passes back along the length of the body; this cord is the nerve chain. The cœlom or body cavity lies between the alimentary canal and the body-wall (Fig. 76), but, as will be seen later, it may become almost obliterated. A similar section through the body of a Vertebrate shows the same limiting body-wall with the two invaginations at either extremity, and the alimentary canal dilated at one portion of its course to form the stomach. Dorsally to the digestive tube there is situated a rod-like body, the axial skeleton (notochord or vertebral column), and more dorsally still, the nerve chain, in the form of a single hollow tube dilated at the anterior end to form the brain. The heart lies in the cœlom ventrally to the alimentary canal.

The Vertebrata are thus characterized by the ventrally situated heart, the unpaired, hollow, and dorsally placed nerve cord, and by the presence of a dorsally situated skeletal rod. The Invertebrata are contrasted, by their dorsally situated heart, their paired and solid nerve cord, and the absence of an internal, dorsal, supporting skeletal rod.

As already mentioned, *Hydra* is composed of two structural layers only, i. e. an endoderm and ectoderm, while the higher forms are composed of three, i. e. endoderm, mesoderm, and ectoderm. Hence we may divide the Metazoa into the **Diploblastica** and the **Triplo-**

blastica. There is, however, no definite demarcation between the two divisions, for some Medusæ show the formation of an incipient mesoderm, by the wandering of certain cells into a position between the endoderm and ectoderm; it is not possible to state definitely, whether these wandering cells are derived from the one or the other of the two layers, or from both.

CHAPTER III

THE COMPARATIVE MORPHOLOGY OF THE ORGANS OF SCYLLIUM, RANA, AND LEPUS

THE SKELETON.

THE skeleton is the supporting framework of the body, and in the Vertebrate types with which we have to deal, *Amphioxus* excepted, it consists of a **vertebral column or backbone**; a **pectoral girdle** supporting a pair of anterior **limbs** or **extremities**; a **pelvic girdle** supporting a posterior pair of **limbs**; and a **skull** situated at the extremity of the vertebral column.

The skeleton of all Craniate[1] Vertebrates above the lowest fishes passes through three stages in its development: (1) a **membranous stage**; (2) a **cartilaginous stage**; (3) an **osseous or bony stage.** With the exception of the notochord or primitive backbone, which is developed from hypoblast, the skeleton always originates from the middle germinal layer or mesoblast.

THE VERTEBRAL COLUMN.

Dogfish. The vertebral column of the dogfish remains cartilaginous throughout life, and is made up of a number of segments called **vertebræ** (Fig. 1). Each vertebra is composed of a bi-concave cartilaginous disc (Fig. 1, B′ & C) called the **centrum** (C), which is pierced through the centre by a small canal. Arising on either side from the dorsal surface of the centrum are two cartilaginous plates, the **vertebral plates** (V.P), which enclose a tubular groove (N.C) between them; this groove is converted into a closed tube, by the presence of a cartilaginous plate above, called the **neural spine** (N.S), which

[1] Vertebrates that possess a cranium.

is wedged in between the dorsal ends of the vertebral plates. Owing to the fact that the vertebral plates are not as wide as the centrum from which they arise, there exists a gap between the plates of each succeeding vertebra when they are in position; these gaps are filled by hexagonal plates of cartilage called **inter-vertebral plates** (I-V.P). The posterior borders of these plates are notched (F.D.R) for the exit of the dorsal roots of the spinal nerves, while similar notches (F.V.R) in the corresponding borders of the vertebral plates allow the passage of the ventral roots.

Owing to the fact that the vertebræ are bi-concave in form, there exists a bi-convex cavity between each of them, when they are arranged in position (Fig. 1, C). This cavity is filled in the fresh skeleton with a jelly-like material (NO), which is continuous from cavity to cavity through the small canal that pierces the centre of the centrum; this material is the persistent notochord, which has become metamerically constricted along its whole length by the invasion of the cartilaginous centra in the course of their development.

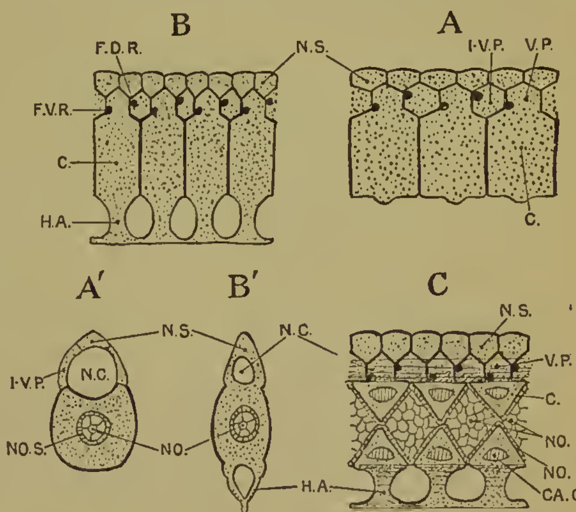

FIG. 1. A. Side view of the Dogfish's vertebral column (trunk or body region). B. Similar view of the caudal or tail region. C. Median vertical section of three caudal vertebræ. A′. End view of a trunk vertebra. B′. Same view of a tail vertebra. C = centrum; CA.C = calcified cartilage; F.D.R = foramen for exit of dorsal root of spinal nerve; F.V.R = foramen for ventral root; H.A = hæmal arch; I-V.P = inter-vertebral plate; N.C = neural canal; NO = notochord; NO.S = notochordal sheath; N.S = neural spine; V.P = vertebral plate.

Vertebræ that are bi-concave are known as **amphicœlous vertebræ**, and are very characteristic of fishes.

The vertebral column of the dogfish may be divided into two regions: **trunk** and **caudal regions**, distinguished by the character of the vertebræ. The trunk vertebræ possess only one arch, the **neural arch** (Fig. 1, A′), while the caudal vertebræ possess a ventral one in addition, the **hæmal arch** (Fig. 1, B′, H.A). The neural arch

bounds the neural canal (N. C) in which the spinal cord is lodged, and the hæmal arch carries the caudal artery and vein.

Development of Dogfish's Vertebral Column. The true morphological nature and significance of the vertebral column cannot be understood without a knowledge of the principal facts of its development. The forerunner of the adult vertebral column is the **notochord** (Fig. 15), which is an elastic rod that appears first in the dorsal roof of the primitive alimentary canal, but which very soon becomes constricted off from that, to form a rod-like body running from beneath the hind brain to the extremity of the tail. It is cellular in substance, but the cells very quickly become vacuolated (Fig. 56), and from the peripheral ones there are secreted two sheaths, an outer **primary** and an inner fibrillar **secondary** one ; the latter is absent in *Amphioxus*. Although formed from the hypoblast, the notochord very shortly after its separation from the alimentary canal lies embedded in mesoblast, and from this there is developed around the notochord a thick membranous layer, the **mesoblastic skeletogenous layer** (membranous stage) ; so that the unsegmented primitive notochord is now enclosed in an unsegmented membrane, which dorsally extends around the spinal cord as well. Within this membrane cartilage is developed as a series of metamerically arranged rings, which thus divide the column into vertebral and inter-vertebral regions ; each ring constitutes the vertebral region and will later give rise to the centrum of a vertebra. In the vertebral regions the cartilage grows inwards and constricts the notochord, while in the inter-vertebral regions (the region between two vertebræ) the notochord remains unconstricted, so that in median longitudinal section (Fig. 1, C) the notochord presents the appearance of a series of hour-glasses applied end to end. The mesoblastic skeletogenous layer in the inter-vertebral region becomes converted into ligament, which serves to hold the centra of the vertebræ together. The cartilage forming the surfaces of the concave faces of the centra, which have arisen from the cartilaginous vertebral rings, becomes calcified : that is, lime salts are deposited in it, but true bone is not formed, and it is not therefore a process of ossification. In the dogfish, from the vertebral column of which Fig. 1 was copied, the calcareous salts (CA.C) were deposited, not upon the surfaces of the centra, but within their deeper substance, the surfaces remaining cartilaginous. Probably there is some variation in this matter. From the dorso-lateral surface of each centrum there arises on either side a cartilaginous ridge, the **vertebral process**,

which later meets and fuses with a cartilaginous plate independently formed in the skeletogenous layer on either side of the spinal cord, and which is the **vertebral plate** (V.P). The **neural spines** and **inter-vertebral plates** also independently arise in the skeletogenous layer, the former along its dorsal margin and the latter at the sides of the spinal cord between the vertebral plates. Each vertebra is thus composed of four pieces, i.e. the **centrum**, the two **vertebral plates**, and the **neural spine**, each of which arises separately in the mesoblastic skeletogenous layer.

Frog. The vertebral column of the frog exhibits a considerable advance upon that of the dogfish, in that it is completely ossified (the cartilage is wholly replaced by bone) and that the first and last vertebræ are specially modified. It is composed of nine vertebræ and terminated posteriorly by an elongated **urostyle** (Fig. 9, U); the latter almost certainly represents two confluent vertebræ, and possibly more, since the tenth spinal nerve passes out from an opening in its anterior fifth, and the ganglion of the nerve lies in the canal within it. This conclusion is based upon the fact that along the length of the vertebral column the number of spinal nerves corresponds to that of the vertebræ, and passes out between them, so that the fact of a spinal nerve passing out from any part of the urostyle would seem to suggest that the point of exit was once the line of articulation between two vertebræ, which have subsequently fused together. Of the nine vertebræ, the first one, that with which the skull articulates, differs from the others and is distinguished as the **atlas**. It bears no transverse processes, its centrum is very much compressed, and on its anterior face, at the base of the neural arch, there are two oval facets, which are of the nature of modified transverse processes, one on either side of the centrum, for articulation with the two occipital condyles of the head; in other respects it resembles the other vertebræ. The other eight vertebræ are almost exactly alike, with the exception of the third and ninth, which only differ from the others in certain small details, and hence a description of one will answer for them all.

The **centrum** or **body** (Fig. 2, A & B, C) is compressed from the front to back, its anterior face is concave and its posterior convex, the latter face fitting into the concavity of that of the vertebra next behind (Fig. 2, B). From either side of the centrum there arises a bony plate, the **neural process** or **neurapophysis**, which, meeting its fellow of the other side in the mid-dorsal line, forms the **neural arch**, the dorsal summit of which very slightly projects as the

neural **spine** or **spinous process** (Fig. 2, N.S). Projecting outwards from the sides of the neural arch, on either side, is a semi-cylindrical, **transverse process** (T.P), the development of which tends to show that it corresponds to the ribs of other animals, since it arises independently of the vertebra itself, and subsequently becomes fused with it. The outer upper corners of the posterior and anterior ends of the neural arch slightly project to form articular surfaces, for articulation with the vertebræ next in front and behind; those of the posterior end (Fig. 2, P.Z) look downwards and outwards and articulate with those of the anterior end (Fig. 2, A.Z), which look upwards and inwards, of the vertebra next behind. These articular surfaces are called **zygapophyses, posterior** and **anterior** respectively.

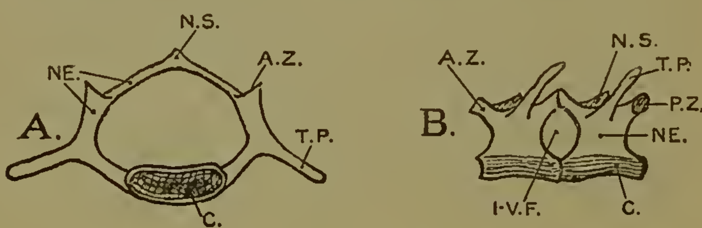

FIG. 2. A. Anterior view of third vertebra of Frog's vertebral column. B. Side view of fifth and sixth vertebræ; A.Z = anterior zygapophysis; C = centrum; I-V.F = inter-vertebral foramen for passage of spinal nerve; NE = neurapophysis (neural arch); N.S = neural spine; P.Z = posterior zygapophysis; T.P = transverse process.

The third vertebra has large expanded transverse processes which are ventrally directed to a greater extent than in the other vertebræ.

The ninth vertebra (Fig. 9) has also much expanded transverse processes, which are directed more posteriorly than those of the other vertebræ, and which serve to support the pelvic girdle at their extremities. The posterior face of the centrum has two lateral convex surfaces for articulation with the urostyle, instead of a median one, as in all the vertebræ in front.

Owing to the almost identical nature of the vertebræ, the vertebral column of the frog shows no very marked distinction into parts, and the only one that can be made is that which divides it into **pre-sacral, sacral**, and **post-sacral**. The ninth vertebra alone forms the sacral region and gives attachment to the pelvis, and all the vertebræ in front of it constitute the pre-sacral region, while the urostyle behind it forms the post-sacral region.

The facts of development show that the first (most anterior) vertebra of the frog becomes merged with the base of the skull to

form the occipital region, so that the atlas of the adult is not the first, but the second vertebra, and is not, therefore, homologous with the vertebra of the same name of higher Vertebrates. But although during the development of Vertebrata higher than the frog, no direct evidence is presented of a fusion of some of the anterior vertebræ with the base of the skull, it must not be forgotten that the developmental history of the skull of but a comparatively few is known, and there are other reasons for believing that the occipital region of the mammalian skull is composed of the confluent first two vertebræ. In the lower Vertebrata, different stages in the act of merging can be seen in several bony fishes (cod, haddock, &c.); and whereas in the frog the hypoglossal nerve is the first spinal nerve, passing out from the spinal cord between the first and second vertebræ, in the rabbit it is the twelfth (last) cranial nerve and passes out through the base of the skull. It would appear, therefore, that in the latter, owing to the confluence of the first two vertebræ with the skull, the hypoglossal nerve has been apparently shifted forward, and while retaining its original position in relation to the original vertebræ, it now appears to pass out from the base of the skull, because that probably represents the two confluent vertebræ. Hence we are justified, in the absence of direct observation, in concluding that the occipital region of the skull of mammals is composed of two vertebræ. If this conclusion is correct, then the atlas of the frog, which we know to be in reality the second vertebra, is homologous not with the atlas of the rabbit, but with the base of its skull; and the apparent second, in reality third, vertebra of the frog is homologous with the atlas of the rabbit.

Rabbit. The vertebral column of the rabbit exhibits a very great advance in detailed organization upon either that of the frog or dogfish. The column is wholly bony, with the exception of the intervertebral ligaments; the anterior and posterior faces of the centra are flattened and bear disc-like pieces of bone upon them, called the **epiphyses**, which remain free and independent of the centra for some time after birth, but subsequently become merged with them (Fig. 3, D, E). They are very characteristic of the backbone of mammals, with the exception of the lowest, in which they are but imperfectly developed.

The vertebral column is very distinctly marked into regions, by differences in the vertebræ themselves; these are called the **cervical**, **thoracic**, **lumbar**, **sacral**, and **caudal regions**, and consist of seven, twelve, seven, four, and fifteen vertebræ respectively.

Any of the first six thoracic vertebræ may be regarded as the most

typical, to which the others may be compared or contrasted, so that we shall first describe one of these and subsequently the others. Such a vertebra (Fig. 3, D & E) is made up of the same elements and

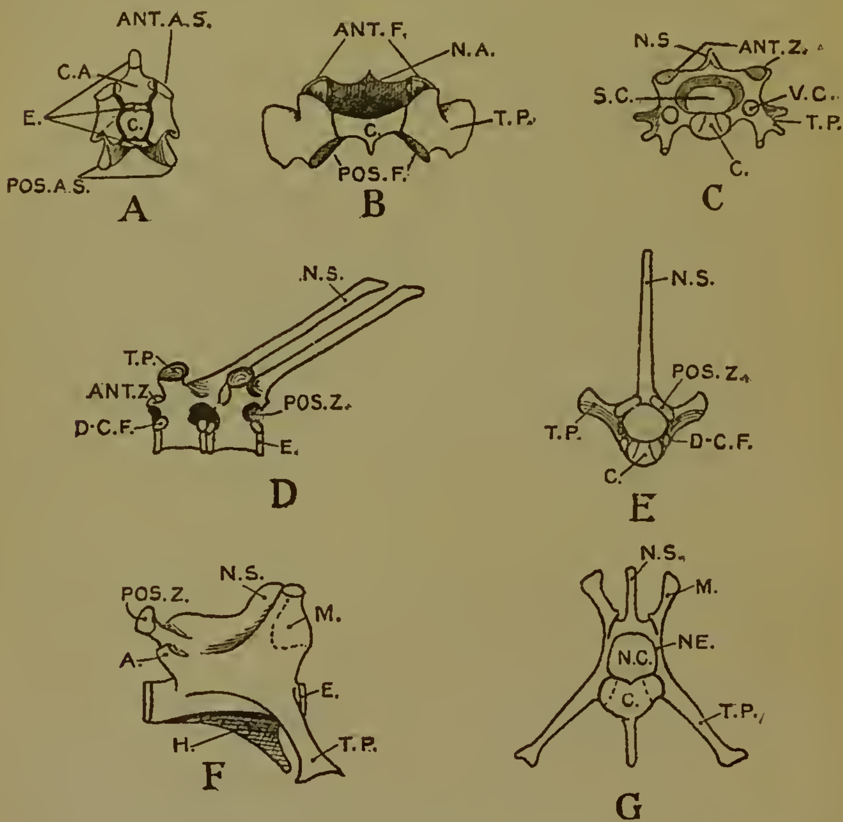

FIG. 3. Vertebræ of the Rabbit. A. Axis (2nd) of a very young animal in which the parts are not merged together, and showing that the odontoid peg C.A arises as a separate piece (*ventral view*). B. Atlas (1st) of a young animal, in which the centrum C still remains separated from the neurapophysis (*ventral view*). C. Anterior view of a cervical vertebra. D. Lateral view of 5th and 6th thoracic vertebræ. E. Posterior view of one of the same. F. Side view of a 1st lumbar vertebra. G. Anterior view of same. A = anapophysis; ANT.A.S = anterior articular surface; ANT.F = anterior facet; ANT.Z = anterior zygapophysis; C = centrum; D-C.F = demi-capitular facet; E = epiphysis; H = hypapophysis; M = metapophysis; N.A = neural arch; N.C = neural canal; NE = neurapophysis (neural process); N.S = neural spine; POS.A.S = posterior articular surface; POS.Z = posterior zygapophysis; POS.F = posterior facet; S.C = spinal (neural) canal; T.P = transverse process: the index line in C points to the ventral limit of the process, and the process ventrad of it is the vestige of the cervical rib; V.C = vertebrarterial canal.

built upon the same plan as any of those of the frog. The centrum (C) is a trihedral mass of bone, compact throughout, and containing no trace of the primitive notochord, such as exists, in some cases

throughout life, in the centra of the frog's vertebræ. Arising from either side of the centrum is a bony plate, the **neural process** or neurapophysis (NE), which passes dorsally and meets its fellow of the other side, in the middle line, to form the **neural arch.** The canal enclosed by the neural arch is the neural canal (N.C), and the spinal cord is lodged in this.

The dorsal summit of the neural arch bears a backwardly directed, long spinous process, the **neural spine** (N.S). From either side of the neural process there arises a short stout rod, the **transverse process** (T.P), directed outwards, and bearing at its free extremity an articular surface, the **tubercular facet**, for articulation with one of the tubercles of the ribs: in Fig. 3, D, the index line of T.P points to the facetted surface. The upward and outwardly directed portion of the neural process projects anteriorly in the form of a small obliquely horizontal process, the **anterior zygapophysis** (ANT.Z); posteriorly there is a similar projection to form the **posterior zygapophysis** (POS.Z). The former looks upwards and inwards and the latter downwards and outwards; they are articular surfaces that allow of a certain amount of movement of the vertebræ upon each other, and are so disposed that the anterior pair of any vertebra works on the posterior pair of the one next in front. The posterior border of the neural process has a deep notch, the **inter-vertebral foramen**, cut in it, beneath and in front of the posterior zygapophysis, in order to allow of the transit of the spinal nerve of that segment.

The vertebral articulation of the ribs. Each of the twelve thoracic vertebræ bears ribs, the anterior seven of which are connected at their other extremity with the sternum (Fig. 4, S.R), while the two next behind are only connected with the last one of these; the remaining three have their extremities free, and hence are called 'floating ribs.'

The articulation of each rib is contributed to by the centra of two adjacent vertebræ, and by the transverse process of one of them; the head of each of the ribs is bifid, that is, branched like the two prongs of a fork; and the **tubercular facet** forms an articulation for one of the prongs, while the articulation for the other prong is formed by a small semicircular demi-capitular facet (Fig. 3, D-C.F) at the anterior border of the centrum of the same vertebra, which comes into juxtaposition with a similar facet on the posterior border of the vertebra next in front, the two facets together constituting a single articular surface known as the **capitular facet.** At the **head** of each

of the first seven ribs there is a **tubercle** for articulation with the capitular facet, and a little way back, on its dorsal side, there is another for articulation with the tubercular facet of the transverse process. The ribs can, therefore, by means of these articulations be rotated backwards and forwards; and since the radius of the curve of each rib increases from before backwards, and they are attached to the sternum at their ventral extremity, it follows that each forward movement carries that outwards and thus increases the width of the chest cavity in the dorso-ventral axis; while a backward rotation similarly carries the sternum inwards and decreases the width of the thoracic cavity.

In the last three thoracic vertebræ, i.e. the 10th, 11th, and 12th, the neural spines are flat plates and stand almost vertically, while the transverse processes are much reduced; and dorsally to them there are another pair of processes, the **metapophyses**.

The **cervical vertebræ** (Fig. 3, C) are rendered distinctive by the presence of the **vertebrarterial canal** (V.C), which is formed as the result of the fusion of a vestigial rib with the transverse process (T.P) and centrum (C); during life this canal conveys the vertebral artery. The neural spines (N.S) are flatter and not half as long as those of the thoracic vertebræ.

The first two cervical vertebræ are much modified and need special attention.

Atlas (*first cervical*). This is of the nature of a bony ring (Fig. 3, B), for the centrum is very much compressed and reduced. The anterior border of the neural arch bears on either side, and immediately abutting on the centrum, a deep concavity with a polished surface; these fit the corresponding rounded eminences at the base of the skull, and are known as the **anterior facets** (ANT.F). Posteriorly it bears a pair of **posterior facets** (POS.F), which are slightly concave and look directly inwards towards the middle line; they articulate with the anterior articular surfaces (Fig. 3, A, ANT.A.S) of the second vertebra. The transverse processes (T.P) are broad and flattened.

Axis (*second cervical*). The centrum of this is produced into a peg-like structure, the **odontoid peg** (Fig. 3, A, C.A), which is directed forward and upward; at the base of the peg are the two rounded articular surfaces (ANT.A.S) that work on the posterior facets of the atlas. In the vertebra of a young rabbit (Fig. 3, A) the centrum is seen to be composed of no less than four pieces, and the study of development shows that the odontoid peg is a part of the centrum of

the atlas, which early becomes constricted off from that and becomes fused with the epiphyses and centrum of the axis. The odontoid peg articulates with the inner surface of the centrum of the atlas. The neural spine is greatly produced as a ridge-like structure, which in some instances is slightly bifid behind. The transverse processes are small and directed backwards.

In the **lumbar vertebræ** (Fig. 3, F & G) the transverse processes are very large and long, but bear no tubercular facets, since there are no lumbar ribs. The metapophyses (M) are more strongly developed than in the last three thoracic vertebræ, and the neural spines (N.S) are large and laterally compressed; while from the posterior end of the centrum, just beneath the zygapophysis, there projects, on either side, a small pointed process, the **anapophysis** (A). The first and second lumbar vertebræ (Fig. 3, F, H) each bear a ventral process, the **hypapophysis**.

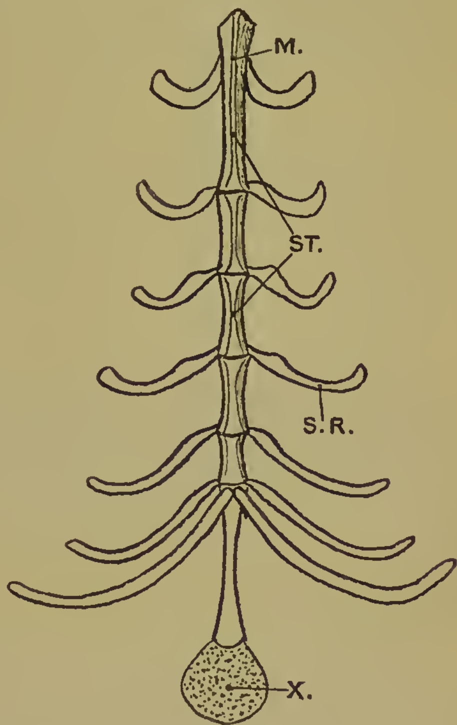

FIG. 4. Ventral view of sternum of Rabbit. M = manubrium; ST = sternabræ; S.R = sternal ends of ribs; X = xiphisternum.

The **sacral vertebræ** (Fig. 10) vary greatly in size, the first and second being large, while the third, and especially the fourth, are small. The first one, and to a much smaller extent the second, gives attachment to the pelvic girdle, the former by means of a much expanded process, comparable to a pair of sacral ribs which have become merged with the vertebra. The processes are much reduced, and the anapophyses and hypapophyses are absent. The four sacral vertebræ are firmly united to each other by synostosis; in strictness, only the anterior two, which give attachment to the girdle, and between which some of the nerves that form the sciatic plexus pass, ought to be considered as sacral vertebræ;

the hinder two are probably caudal vertebræ, which have become united to them.

The **caudal vertebræ** are fifteen in number, the first six of which are like the last sacral, but smaller, and the remainder are merely rods of bone, representing centra only. They are vertebræ in the course of retrogression, the hindermost ones having advanced farthest.

The sternum. The sternum (Fig. 4) of the rabbit consists of six segments united to form a curved rod-like structure. Of these segments, called **sternabræ** (ST), the first is larger than the others, and is distinguished as the **manubrium** (M), while the last is terminated distally by a flat plate of cartilage, the **xiphoid process** (X).

As shown by the study of its development, the sternum is the confluent expanded ventral termination of the ribs. In the course of their development, and during the cartilaginous stage, the ventral ends of the ribs enlarge, and these, meeting the similar enlargements of its fellows of the same side, merge together to form a plate of cartilage. As this takes place upon both sides, the sternum at this stage is represented by two adjacent plates of cartilage, which a little later unite together to form a single plate, in which subsequently six centres of ossification are formed. The xiphoid process similarly represents the fusion of the expanded ends of a pair of ribs, but in this no centre of ossification is formed and it remains cartilaginous throughout life.

The Pectoral Girdle or Arch.

Dogfish. The pectoral girdle is the skeletal organ upon which the anterior or pectoral pair of fins are supported; it consists of a curved bar of cartilage lying in the ventral body-wall, ventrad of the pericardial cavity, and extending upwards round the sides of the body, in close proximity to the last gill arch, to reach the dorsal surface of the body. It is divided into a dorso-lateral **scapular region** (Fig. 5, S.C & S-S.C) and a ventral **coracoid region** (C.C) by a ridge which bears the articular surface for the fin. The scapular region may be itself divided into a lateral scapular one (S.C) and a dorsal suprascapular (S-S.C). The pectoral arch of the dogfish is thus very simple and primitive.

Frog. The pectoral arch of the frog is much more complicated than that of the dogfish, and there are structures connected with it which the study of development shows do not properly belong to it. The arch or girdle is at first, in the early stages of develop-

ment, composed of two plates of cartilage, one on either side of the body, that meet in the middle line, and each of which is divided

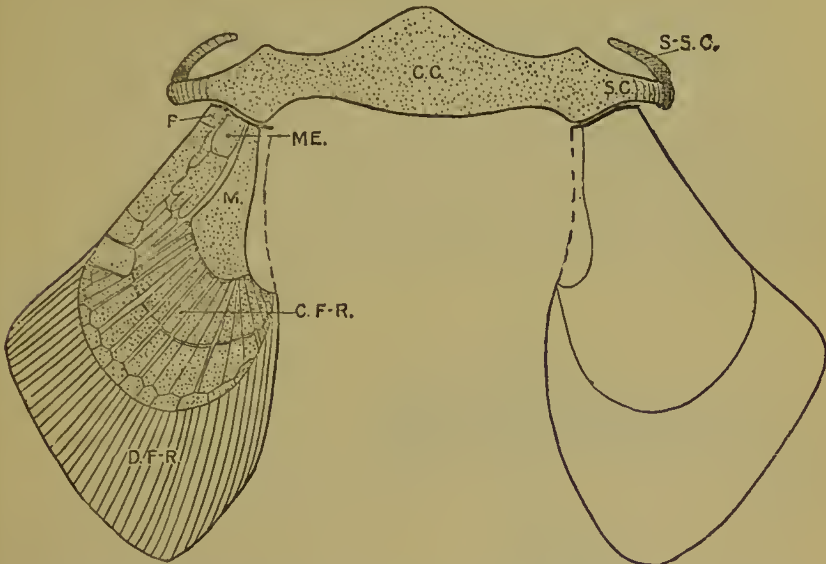

FIG. 5. Pectoral girdle and fins of *Scyllium* (Dogfish). The outline only of the left fin is represented. CC = coracoid cartilage or region; SC = scapular cartilage or region; S-S.C = supra-scapular cartilage or region; M = metapterygium cartilage; ME = mesopterygium cartilage; P = propterygium cartilage; C.F-R = cartilaginous fin-rays; D.F-R = dermal fin-rays. It is preferable to speak of regions rather than cartilages when dealing with the girdle, because individual cartilages do not exist, and we can at most only distinguish regions corresponding to the distinct elements of the girdle of other animals.

into a dorsal scapular and a ventral coracoid portion by a concave depression called the glenoid cavity (Fig. 6, G.C), which serves for the articulation of the humerus of the arm. At this stage, therefore, the arch is fundamentally the same as that in the dogfish, except that from the first the coracoid portion is split into two diverging forks, a posterior or **coracoid** propcr (Fig. 6, C), and an anterior or **precoracoid** (P). Later, the scapular region becomes marked off into a dorsal flat expanded cartilage, the **supra-scapula** (S-S), which remains semi-cartilaginous throughout life, and a ventro-lateral more rod-like portion, the **scapula** (SC), the primitive cartilage of which becomes ossified. The coracoid cartilage proper becomes invested with a layer of bone, whilc along the antcrior border of the precoracoid cartilage there is developed a bony rod, the **precoracoid bone or clavicle** (P & C). As to how far we are justified in regarding the so-called claviclc of the frog as a true clavicle homologous to that of higher forms is a matter of dispute. By some it is regarded

merely as a precoracoid bone, in the same sense that the ossification round the coracoid is regarded as a coracoid bone; and the fact that this so-called clavicle is sometimes formed not as a rod-like ossification along the anterior border of the precoracoid cartilage, but as a semi-tubular bone investing that, would seem to justify this conclusion. By others, however, the cartilaginous bar is regarded as the precoracoid and the ossified bar in front of it, or encircling it, as the clavicle. Fig. 6 was copied from a specimen in which the clavicle invested the precoracoid. The coracoids and precoracoids of either side do not meet in the middle line, but are separated by a narrow band of calcified cartilage, known as the **epicoracoid** (Fig. 6, E); it arises by the ventral ends of the coracoid and precoracoid cartilages growing towards each other until they meet, when they become confluent. When ossification round the coracoid and precoracoid takes place, this median portion is not affected by that process, and remains for some time solely cartilaginous; but later, calcareous salts are deposited within it, and it thus becomes converted into a calcified cartilage.

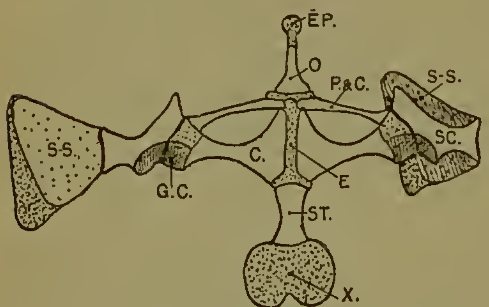

Fig. 6. Pectoral girdle of *Rana* (Frog). On the left of the figure the supra-scapula is represented *in situ*, but on the right as being pulled forwards. C = coracoid; E = epicoracoid; EP = episternum; G.C = glenoid cavity; O = omosternum; P & C = precoracoid and clavicle; SC = scapula; S-S = supra-scapula; ST = sternum; X = xiphisternum. The clavicle is the bone seen in the figure, and the precoracoid is a slender rod of cartilage invested by that, and consequently hidden from a ventral view.

During development, the epicoracoid cartilage grows forward as a small process, which expands at its anterior extremity to form a flat plate-like structure; at its posterior end this becomes segmented off from the epicoracoid, so that it becomes a separate piece; the narrower posterior half of this becomes ossified to form the **omosternum** (Fig. 6, O), while the anterior expanded portion remains cartilaginous throughout life as the **episternum** (Fig. 6, EP).

In the middle line of the ventral abdominal body-wall, immediately behind the posterior border of the coracoids, there is developed a pair of cartilaginous bands; these quickly unite to form a single plate, which later expands considerably in its hinder half. This structure becomes secondarily connected with the pectoral girdle; its anterior

half becomes ossified to form the **sternum** (Fig. 6, ST), while the posterior half remains cartilaginous and constitutes the **xiphisternum** (X). From the mode of its development it can hardly be regarded as an exactly corresponding structure to the sternum of the rabbit, which as we have seen results from the fusion of the expanded ends of the ribs. It may, however, represent the rudimentary basis, from which in the course of evolution the sternum of the higher Vertebrata has been derived and in which the connexion with the ribs may be of secondary origin.

Rabbit. In the pectoral girdle of the rabbit (Fig. 7), almost all the coracoid portion (C) has disappeared, while the scapula (SC) has become relatively more developed and strengthened. The latter is a triangular plate of bone, with its narrowed end pointing forwards and downwards (anteriorly and ventrally) and terminated by a shallow depression, the **glenoid cavity** (G.C), for articulation with the humerus. The anterior portion of the narrowed extremity is produced into a blunt process (E-C.S) which overhangs the glenoid cavity, and is called the **epicoracoid process** (coracoid process of some authors). In the scapulæ of some young rabbits (Fig. 7, C) there is developed a small cubical bone, which lies between the epicoracoid process and the glenoid cavity, and which represents the last trace of the **coracoid** proper: it is worth noting that it is now at that stage of disappearance at which, apparently, the wolf's tooth of the horse has reached, i.e. it only occasionally appears, and is too vestigial to function as a useful organ.

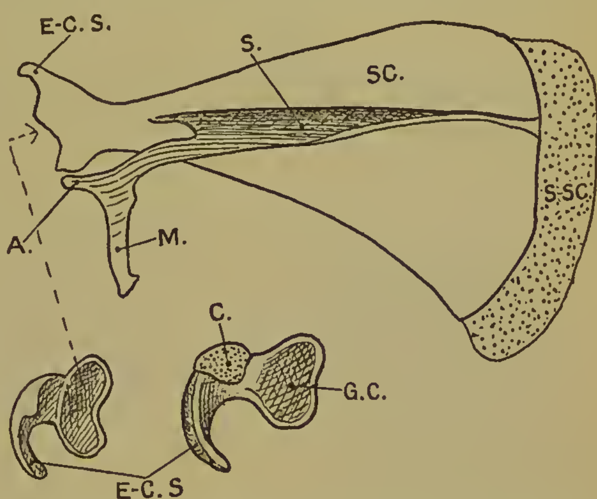

FIG. 7. Pectoral girdle of *Lepus* (Rabbit). A = acromion; C = coracoid; E-C.S = epicoracoid spine; G.C = glenoid cavity; M = metacromion; S = spine of scapula; SC = scapula: S-SC. = supra-scapula. The small figure on the left is a surface view of the glenoid cavity of an old rabbit, and that to its right, a similar view of the girdle of a young rabbit (six weeks), showing the independent coracoid ossification.

The dorsal border of the scapula is limited by a narrow plate of

cartilage, the **supra-scapula** (S-SC), and there extends along the outer surface of the scapula a triangular ridge called the **scapular spine** (S), which is produced ventrally into a blunt process, the **acromion** (A), from the posterior border of which a longer spine, the **metacromion** (M), projects. The spine and processes afford points of insertion for some of the strong muscles that move the anterior limbs.

The **clavicle** is much reduced, and is represented by a slender rod-like ossification and three small nodules of cartilage in the ligament running from the acromion to the sternum. It is not a membrane bone, as until recently it was thought to be, but a cartilage bone, i.e. bone formed in cartilage and not in the investing membrane.

Pelvic Girdle or Arch.

Dogfish. The pelvic arch of the dogfish is very simple, consisting of a transversely arranged bar of cartilage (Fig. 8). The articulation

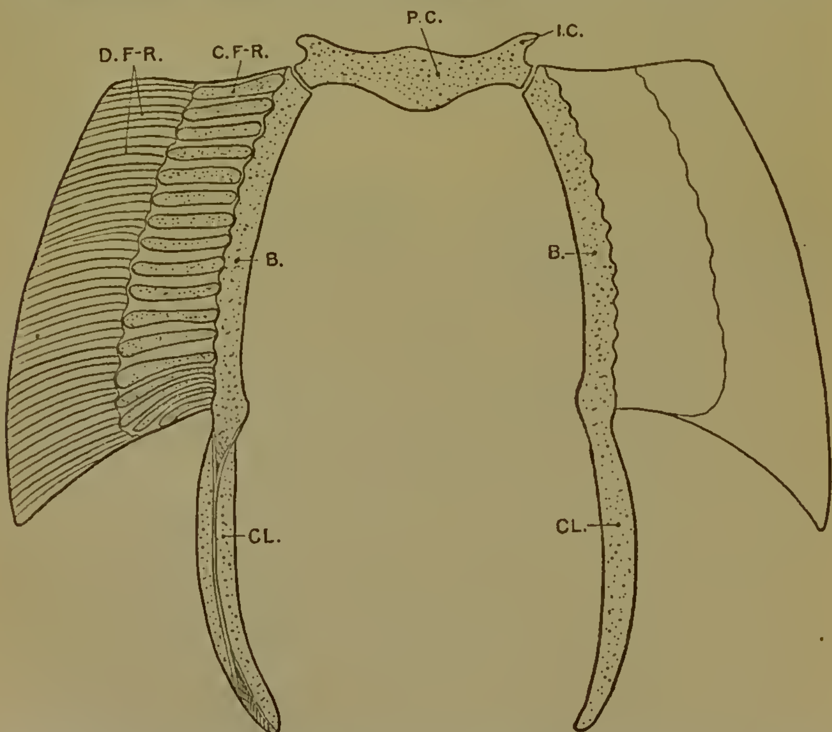

Fig. 8. Pelvic girdle and fins of a male Dogfish (*Scyllium*). The left fin is represented in outline only. P.C = pubic cartilage or region; I.C = iliac cartilage or region; B = basipterygium; CL = claspers; C.F-R = cartilaginous fin-rays; D.F-R = dermal fin-rays.

for the basal elements (B) of the fin lies upon the outer and posterior extremity of either side and divides each half of the girdle into a dorsal **iliac** portion (I.C) which is very small, and a ventral pubic part (P.C). In its development the pelvic arch is very similar to that of the pectoral, consisting of two bars of cartilage, one on either side, which later merge together in the middle line, and which are at first continuous with the basal element of the fins. It is worth noting also, that the iliac portion is much larger in the embryo than in the adult, and that it is directed forward along the long axis of the body, so that, although it is very simple in its adult structure, it does not represent the most primitive condition. It specializes in the course of its development, by a reduction in size of the iliac process, and by the alteration of the plane in which that lies.

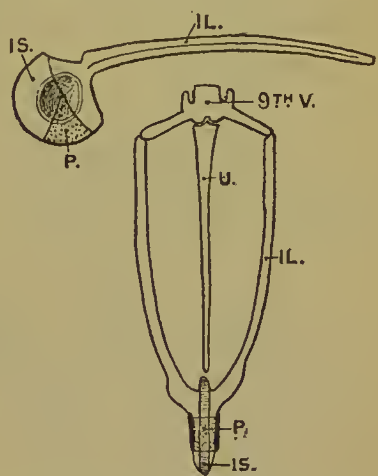

FIG. 9. Pelvic girdle of Frog (*Rana*). The top figure represents a side view and the bottom one a ventral view. IL = ilium (iliac); IS = ischium; P = pubis; U = urostyle.

Frog. The pelvic girdle of this animal is very much specialized, i. e. modified for the more effectual performance of certain activities. It consists of three parts on either side, of which the two posterior merge with each other to form a single piece. The **iliac** (Fig. 9, IL) is an elongated bone, articulated at its anterior end with the expanded ribs of the sacral vertebra (V); posteriorly it enlarges, and receives the bony **ischium** (IS) and the cartilaginous **pubis** (P), and also forms the anterior portion of the **acetabulum** or concavity for articulation with the femur. The acetabulum is equally contributed to in its formation, by the pubis, ischium, and ilium (iliac).

In its early stages of development, the pelvic girdle is not longer than the pectoral, and like that, it lies at right angles to the long axis of the body; but as the hind limbs lengthen, the acetabular portion of the girdle rotates backwardly and assumes a dorsal position, and at the same time the iliac lengthens considerably, so that the pelvic girdle now forms an elongated organ lying parallel, or nearly so, to the vertebral column. At first, also, the right and left halves are quite distinct from each other, but very soon fuse together at their

expanded ventral ends (which becomes the posterior of the adult). Thus the specialization of the girdle is in the direction of a very great elongation of some parts, a fusion of others, with a dorsalwards rotation of the whole. This results in the production of a greater leverage and rigidity of the parts, with an alteration in the position of the fulcrum, adapted to the jumping mode of locomotion of the animal.

Rabbit. The pelvis of the rabbit is composed of two parts united in the mid-ventral line by a cartilaginous **symphysis pubis** (Fig. 10, S.PU); each half is known as an **innominate bone** (IN.B) and consists of three bones, i.e. the **iliac** (IL), **ischium** (IS), and **pubis** (PU), together with a small **cotyloid** (CO) or **acetabular bone**, which probably represents the epiphysis of the pubic bone. In the young animal, these bones are free from one another and meet in a tri-radiate suture in the centre of a deeply concave articular surface, the **acetabulum** (ACE), but later, they unite by synostosis to form the single innominate bone. The pubis alone takes part in the formation of the symphysis pubis. By the ventral union of the pubis and ischium the **obturator foramen** (OB.FOR) is formed. The ilium is broad anteriorly and a portion of its inner surface is roughened to form an attachment for the sacrum (1st SAC).

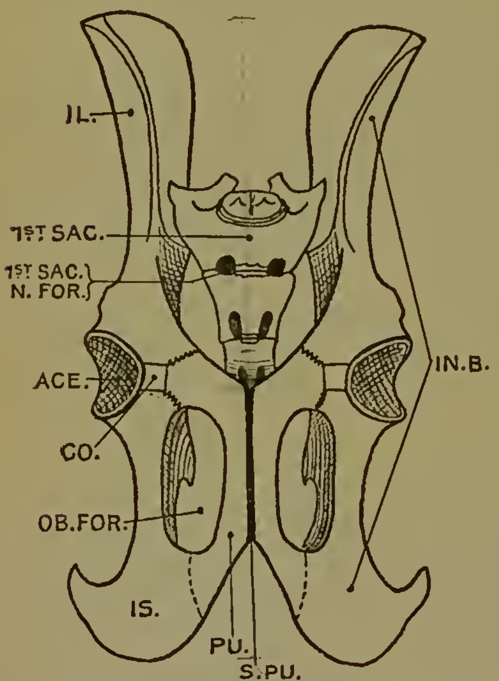

FIG. 10. Pelvic girdle of Rabbit (*Lepus*). Ventral view. ACE = acetabulum; CO = cotyloid bone; IL = ilium (iliac); IS = ischium; IN.B = innominate bone; PU = pubis; OB.FOR = obturator foramen; S.PU = symphysis pubis; 1st SAC = first sacral vertebra; the second and third sacral vertebræ are represented behind the first. 1st SAC.N.FOR = foramen of exit for first sacral spinal nerve. The dotted line between PU and IS represents the plane of fusion of the ischium and pubis, which occurs very early.

In the adult, the pelvic girdle lies in a plane nearly parallel to the vertebral column, but in the embryo it is nearly at right angles

to it and attains the adult condition by backward rotation. Primitively it consists of a single plate of cartilage, in which there are subsequently developed the three centres of ossification of the ilium, ischium, and pubis.

The acetabulum is formed by all the three bones, but the pubic bone is almost completely cut out from its formation by the cotyloid bone.

The Limbs or Extremities.

Anterior Limbs or Arms.

Dogfish. The **pectoral fin** (Fig. 5) is composed of three **basal cartilages** which support a series of narrow cartilaginous **fin-rays** (C.F-R). Of the basal cartilages the inner is much the largest and is called the **metapterygium** (M), and it supports by far the greater number of the fin-rays; the next outer cartilage, the **mesopterygium** (ME), is much smaller and is followed outwardly by the **propterygium** (P).

The study of development shows that the basal cartilages and fin-rays are derived from a single plate of cartilage, which in the early stages is continuous with the pectoral arch. The single plate of cartilage at a very early stage becomes split into a number of parallel rays, at right angles to its length, and which remain continuous with it. The unsegmented part of the plate is called the **basipterygium**. A little later, the latter becomes divided into a larger posterior (inner) portion, the **metapterygium** and a smaller anterior portion; the latter becomes at a slightly later stage divided into two, a posterior portion, or **mesopterygium**, and a smaller anterior part, the **propterygium**. While the division of the basipterygium into three parts is proceeding, the parallel rays become segmented off from it, to form the **cartilaginous fin-rays**, and at the same time it itself becomes segmented off from the pectoral girdle.

Frog. Between the condition of the fin of the dogfish and the limb of the frog, there is an immense structural gulf which has not been bridged by either embryology or palæontology; nevertheless it is possible to conceive of the manner by which the latter could have been derived from the former. The plan of structure of the limbs of the frog is fundamentally the same as that of all higher Vertebrates, i.e. of reptiles, birds, and mammals, and is equally fundamentally different from anything exhibited by the fins of fishes.

The arm proper, or the first portion of the limb, is composed of one bone, the **humerus** (Fig. 11). It is cylindrical in form and terminated at its two extremities by a rounded articular head (H), the anterior one of which works in the glenoid cavity, while the posterior articulates with the proximal end (OL) of the forearm. Along the ventral surface of the anterior half of the humerus there runs a well-developed ridge called the **deltoid crest** (D.C′), and in the male upon the dorsal surface of the posterior half there is a similar ridge, the **median crest** (M.C) ; the latter is absent in the female.

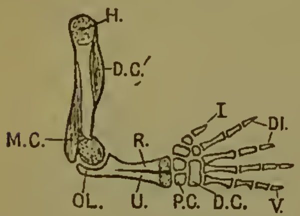

FIG. 11. Anterior limb or arm of Frog (*Rana*). H = proximal head of humerus; D.C′ = deltoid crest; D.C = distal carpalia; DI = digits; M.C = median crest; OL = olecranon process; P.C = proximal carpalia; U = ulna; R = radius; I–V = first to fifth digits.

The forearm is composed of two bones fused together along their whole length, the double nature of which is indicated by a shallow median constriction (Fig. 11). Of these two bones, that which lies along the inferior (under) side is called the **radius** (R), and the other the **ulna** (U); the latter is prolonged anteriorly beyond the hollowed articular surface as a small **olecranon process** (OL). The forearm being thus of a compound nature is known as a **radio-ulnar.** The extremity of the forearm which works upon the humerus is known as the **proximal end**, and that at the other end which receives the bones of the wrist is called the **distal end.** These terms apply to any structures that have two extremities one of which is situated nearer (proximally) to a central organ than the other more distally placed.

Wrist or Carpus. A proper conception of the typical nature of the wrist cannot be obtained by the isolated study of the frog alone, and we shall first proceed to study a more typical form.

If we examine the prepared skeleton of the wrist of the common green lizard, we shall find that it consists of ten small nodular bones (in reality calcified cartilages), which are arranged in the following manner. At the distal end of both the radius and ulna there is situated one row of three small bones, each of which is known respectively as the **radiale** (articulating with the radius), the **ulnare** (articulating with the ulna), and between them is wedged in the much smaller one, the **intermedium.** Distally to this row of carpal bones, there is another row composed of five bones and known as the first, second, third, fourth, and fifth **carpalia**, the first being situated upon

the radial side. The first row of three carpal bones is called the **proximal row** or **proximal carpals**, and the other row of five bones the **distal row** or **distal carpals**. Wedged in between the proximal and distal rows is another bone, the **centrale**, which forms by itself a middle row. The tenth carpal bone is attached to the outside of the distal extremity of the ulna, and is called the **pisiform** or **accessory ossicle**. Articulating with the distal surfaces of the distal row of carpals are five long bones, the bones of the middle hand, called the **metacarpals**, and which in their turn bear the fingers or **digits**. Each finger is composed of several elongated bones, each of which is called a **phalange**.

In the frog (Fig. 11) the proximal row of carpals (P.C) consists of a radiale and ulnare, but the intermedium is absent[1]. In the distal row (D.C) there are only three distal carpals instead of five, of which the third is the largest and supports the third, fourth, and fifth metacarpals; it probably therefore represents three confluent carpals. The centrale has shifted its position and lies on the outside of the carpus to the radial side of the radiale. Of the metacarpals, the second, third, fourth, and fifth are long, but the first (Fig. 11, I) is very small and bears no digit; the others bear upon their distal extremities their respective digits (DI), each of which consists of rod-like bones called **phalanges**. There are two phalanges in the second and third, and three in the fourth and fifth (V) digits; hence the **phalangeal formula** is 0.2.2.3.3.

Rabbit. The arm proper of the rabbit, like that of the frog, consists of one bone only, the **humerus** (Fig. 12). It is a cylindrical slightly curved bone, thicker at its proximal than its distal end, and bearing at the former extremity a rounded **head** (H) for articulation with the glenoid cavity; on either side of this there is a somewhat rounded eminence, the **greater** (on the outer side), and **lesser** (on the inner side) (L.T) **tuberosity**. At the distal extremity is a pulley-like surface called the **trochlear** (T), for articulation with the ulna and radius of the forearm (U & R), and to the outer (pre-axial) side of this a smaller articular surface, the **capitellum** (CA), for articulation with the radius alone. To the outer side of this is a rounded eminence, the **external condyle**, and on the post-axial side of the trochlear a similar one called the **internal condyle** (I.C). Above the trochlear are two depressions, one in front and one behind, of which the latter

[1] It has probably fused with one of the two proximal carpals, since that is known to be the case in other Amphibians.

is much the larger, and receives the **olecranon process** (O.P) when the fore-arm is extended. These depressions are known as the **supra-trochlear fossæ**, and that which receives the olecranon is further indicated by the term **olecranon fossa** ; the fossæ of either side are connected by a small hole, the **supra-trochlear foramen** (S-T.F).

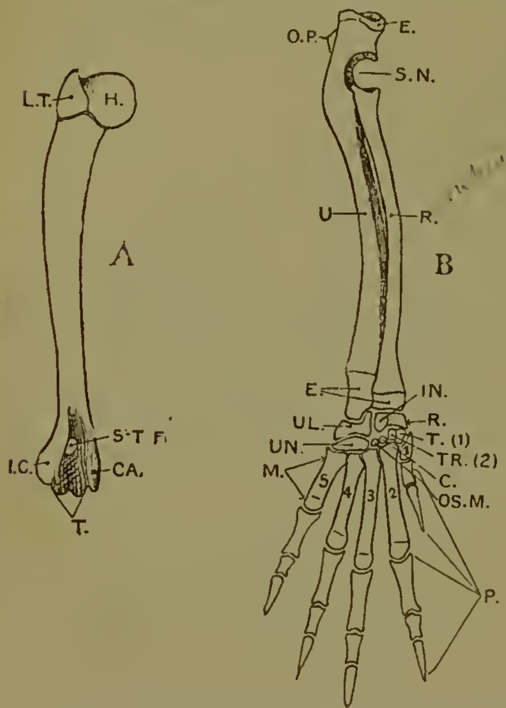

FIG. 12. Arm, fore-arm, and manus (hand) of Rabbit (*Lepus*). Extensor surface. A. Humerus; B. Fore-arm and manus; C = centrale; CA = capitellum; E = epiphysis; H = head; I.C = inner condyle; IN = intermedium; L.T = lesser trochanter; M = metacarpals; OS.M = os magnum; O.P = olecranon process; P = phalanges; R = radiale; S.N = sigmoid notch; S-T.F. = supra-trochlear foramen; T = trapezoid; U = ulna; UL = ulnare; UN = unciform; 1–5 = first to fifth metacarpals.

The fore-arm of the rabbit is composed of two bones which, while they remain perfectly distinct (Fig. 12, U & R), are immovably fixed upon each other, in consequence of which the acts of pronation and supination of our own hands cannot be performed. Let the student turn his hand so that the palm faces upwards, that is pronation; when the palm is downwards it is supination. The change from the one to the other depends upon the rotation of the distal part of the radius round the distal portion of the ulna. The **ulna** is the larger of the two bones, and is situated upon the outer or post-axial border of the fore-arm, and is terminated at its proximal end by a large laterally compressed **olecranon process** (O.P), immediately behind which is the **sigmoid notch** (S.N) for articulation with the humerus. The **radius** (R) is smaller, and its proximal end lies upon the ventral surface of the ulna, but distally it lies to the inner or pre-axial side of that. Both it and the ulna are strongly curved, a character which, in conjunction with the fixation of the two bones, renders it a perfect instrument for purposes of burrowing.

Carpus or **Wrist** (Fig. 12). The proximal row of carpals retains its primitive number, and consists of an **ulnare** (UL), **intermedium** (IN), and **radiale** (R). The distal row (**distalia**) has only four, but of this the large **unciform bone** (UN) represents the fused fourth and fifth distal carpals. The **centrale** (C) is a very small bone, and has slightly shifted its position and appears to belong to the distal row of carpals. On the post-axial side of the palmar surface, and not therefore shown in the figure, is a **pisiform bone** articulating with the ulna and the ulnare.

The **metacarpals** (M) are five in number, of which the first (1) is very short, and the third (3) or middle one the longest. The **phalangeal formula** is 2.3.3.3.3. Sesamoid bones are developed in the tendons of the flexor muscles, at the level of the articulations of the metacarpals and phalanges, upon the palmar surface; they lend support and strength to the tendons in which they are developed.

Posterior Limbs.

Dogfish. The pelvic fin of the dogfish retains a more primitive character than the pectoral fin, since it does not advance beyond the stage of the formation of the basipterygium of that. It consists of a slightly curved bar of cartilage, the **basipterygium** (Fig. 8, B), which supports the parallel **fin-rays** (C.F-R) upon its outer side. In the male, the posterior end of the basipterygium is continued backwards into the rod-like **clasper** (C); this is used as an organ of copulation, and is inserted, together with its fellow of the other side, into the oviduct (one into each oviduct) of the female during sexual union. The remainder of the fin is composed of horny fibres, called the dermal fin-rays (D.F-R).

Frog. The posterior limb of the frog, like the pelvic girdle, is a highly specialized [1] organ, and like that it is specialized in the direction of rigidity of structure and great elongation of certain parts, which adapt it to the attainment of greater jumping powers.

The **femur** (Fig. 13, F) is a long cylindrical bone with a peculiar sigmoid flexure in the middle of its length; it is terminated at either extremity by a rounded head. The succeeding portion of the leg

[1] The student must not accept the term 'highly specialized' as necessarily meaning a high state of organization, for fishes in their way are highly specialized, but with respect to their fundamental organization they are very primitive.

corresponding to our calves consists of two bones of equal length, fused together along their whole extent, and together forming a slightly bent shaft (Fig. 13, T.FI). The two bones composing it are the **tibia** and **fibula**, of which the latter is the outer bone; on account of its constituent bones, this portion of the skeleton of the leg is known as a **tibio-fibula**, and its compound nature is indicated by a fairly deep groove on both surfaces at both its distal and proximal ends. The tibio-fibula is slightly longer than the femur.

The **tarsus** or **ankle**. The two proximal tarsal bones are very much elongated and are quite half the length of the tibio-fibula; the outer one is the **calcaneum** or **fibulare** (C), and the inner one, more strongly curved than the other, is the **astragalus** or **tibiale** (A). The distal tarsals (D.T) are much reduced and consist of only two bony nodules, the larger of which articulates with the second and third digits and represents the fusion of two tarsalia (2nd & 3rd), while the smaller one articulates with the first digit and probably represents the centrale. The fourth and fifth digits articulate directly with the distal extremity of the calcaneum, or rather with a ligament which passes from the larger tarsalia to the proximal end of the fifth metatarsal. To the inner side of the tarsus there are two small nodules (PR), one larger than the other, which probably represent the vestige of a sixth toe; they are known collectively as the **calcar** or **prehallux**. There are five **metatarsals**, that of the **hallux** (I) or great toe being much the shortest, while that of the fourth digit is the longest. The **phalangeal formula** is 2.2.3.4.3.

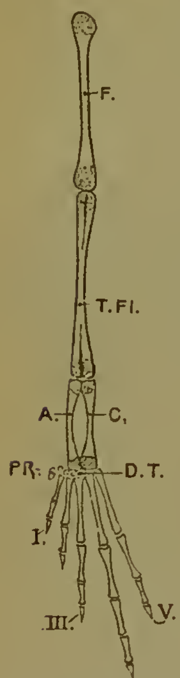

FIG. 13. Posterior limb of Frog (*Rana*). Extensor surface. The sigmoid flexure of the femur is not shown in this view. F = femur; T.FI = tibio-fibula; A = astragalus (tibiale); C = calcaneum (fibulare); D.T = distal tarsalia; PR = prehallux or calcar; I–V = first to fifth digits.

Rabbit. Like that of the frog, the thigh contains a single bone, the **femur** (Fig. 14, A), which is cylindrical and elongated in form, flattened and expanded at its proximal extremity, and thickened and rounded at its distal. The former extremity bears a prominent rounded **head** (H) for articulation with the acetabulum; slightly in front and to the outer side of this is a roughened process, the **great trochanter** (G.T), while

to the inner side and behind it is a ridge-like prominence, the **lesser trochanter** (L.T). Opposite the latter, on the outer border of the femur, is a shorter but thicker ridge, the **third trochanter** (3rd T). Distally there are two prominent condyles (I.C & E.C) for articulation with the **tibia** and **fibula**, separated by a deep and wide groove, the **inter-condylar notch** (I-C.N), continuous with a shallower groove

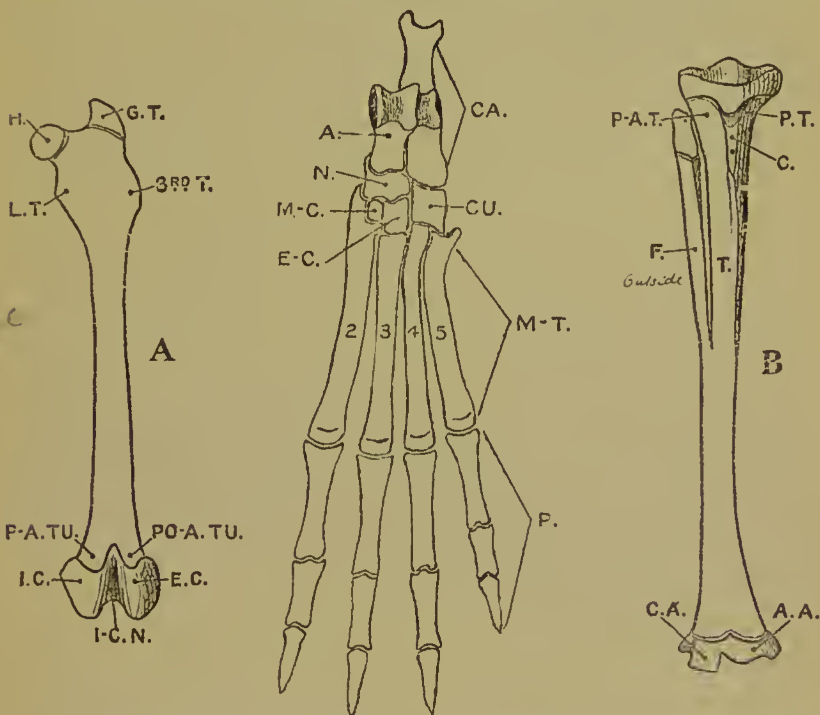

FIG. 14. Posterior limb of Rabbit (*Lepus*). A = left femur (extensor surface); B = right tibia and fibula (extensor surface). The middle figure represents the tarsus and pes (ankle and foot). A = astragalus; A.A = astrageal articulation; C = cnemial crest; CA (upper) = calcaneum; C.A = calcaneal articulation; CU = cuboid; E.C = external condyle; E-C = ecto-cuneiform; F = fibula; G.T = great trochanter; H = head; I.C = internal condyle; I-C.N = inter-condylar notch; L.T = lesser trochanter; M-C = meso-cuneiform; M-T = metatarsals; N = naviculare (centrale); P = phalanges; P-A.TU & P.T = pre-axial tuberosity; PO-A.TU & P-A.T = post-axial tuberosity; T = tibia; 3rd T = third trochanter.

on the front of the bone in which the **patella** or **kneecap** slides. Proximally to the internal and external condyles, are two eminences, the **pre-axial** and **post-axial tuberosities** respectively. At the hinder surface and just above the two condyles are two sesamoid bones, the **fabellæ**; these are bones developed in the tendons of certain muscles for the purposes of support.

The fore-leg (Fig. 14, B) contains two bones, the much greater

tibia (T) and the smaller **fibula** (F), the latter being merged with the former along its distal two-thirds, and its proximal epiphysis fused to a slight extent with the corresponding one of the tibia. The head of the tibia is enlarged and triangular in section, and bears at its proximal extremity two oval surfaces for articulation with the condyles of the femur. The triangular form of the proximal end of the bone is due to the well-developed **cnemial crest** (Fig. 14, C), which extends backwards along the anterior third. At the distal extremity, there is an articular surface for articulation with the **tibiale** (**astragalus**) (A.A) and **fibulare** (**calcaneum**) (C.A).

The **tarsus** or **ankle** (Fig. 14) consists of six bones, arranged in three rows. The proximal row consists of the **calcaneum** (C.A) (**fibulare**) with an articular surface for articulation with the fibula, and behind this a large process, the **calcaneal process** or **heel-bone**. To the inner side of the calcaneum is a smaller bone with a large rounded articular surface, which works upon the corresponding one of the tibia; this bone is the **astragalus** (A) (**tibiale**), and in the rabbit it probably includes also the **intermedium**, which is otherwise absent. The second row contains only the large **naviculare** (N) (**centrale**), which sends a large process along the ventral (plantar) surface of the foot. In the third row, the fourth and fifth tarsalia are fused to form the **cuboid bone** (CU), and next to this is the third tarsal, the **ecto-cuneiform** (E-C), and innermost of all the small **meso-cuneiform** (M-C) (second tarsal).

The metatarsals (M.T) are four in number, and the **phalangeal formula** is 0.3.3.3.3.

The pre-axial or first digit (great toe of man) is absent, and the last trace of it may probably be represented by a small spur on the inner side of the proximal end of the second metatarsal.

The Skull.

Three sets of structures may enter into the composition of the skull, i.e. (1) the **cranium proper**; (2) the **visceral arches**; (3) the **labial cartilages**. All skulls are primitively preformed in membrane (condensed sheets and tracts of mesoblast) within which cartilage may be subsequently formed, either partially or completely. In the skulls of the higher animals, from the bony fishes onwards, the cartilage in turn may be more or less replaced by bone, either formed within the cartilage (**cartilage bone**) or else in the connective-tissue sheath that

invests the cartilaginous skull (**membrane bone**). The ontogenetic history of the skull of the higher animals (birds or mammals) repeats in its successive stages the main morphological advances that the skull presents as we pass from the lower to the higher groups. The most primitive form of skull with which we are acquainted is the lamprey's, and in its fully formed adult condition it is in many features very similar to that of the tadpole, i.e. the embryonic condition of that of the frog. Indeed, the cranium of every craniate animal may be said to be similar in the first portion of its cartilaginous stage to that of the adult lamprey.

No intelligent conception of the nature of the skull is possible without some knowledge of the main facts of its development, and we shall accordingly precede our study of the adult skull by that of its development.

Development of the skull. The primitive nervous system is composed of a tube widely dilated in its anterior region to form the brain. This dilated portion is early marked off into three regions, the fore-brain, mid-brain, and hind-brain, by two constrictions. The hind-brain is continuous posteriorly with the spinal cord, which is supported along its ventral surface by an elastic rod, the notochord, that extends from the posterior extremity of the body up to the level of the middle of the mid-brain, where it ends in a tapering point.

The brain is at first invested in a continuous membranous sheath of mesoblast, and this constitutes the **membranous cranium**, into the base of which the anterior end of the notochord extends.

The first formed cartilage that arises within the investing layer of mesoblast consists of two bars, the **parachordals** (Figs. 15 & 16, P), which arise on each side of the cephalic portion of the notochord and extend forward along it beneath (ventrally to) the hind- and mid-brain. At first these bars are independent of each other and of the notochord, but they soon fuse together to form a continuous plate, the **basilar plate**, in which after a time nearly all trace of the notochord disappears. Very soon after the formation of the parachordals there arises in front of them and in the floor of the membranous cranium, beneath the fore-brain, another pair of cartilaginous bars, the **trabeculæ cranii** (Figs. 15 & 16, T), which extend backwards and meet behind at the anterior extremity of the notochord, which they embrace. In the dogfish the trabeculæ are at first distinct from the parachordals, but later fuse with their anterior extremities to form a continuous piece. In the frog (Fig. 16), chick, and rabbit the

trabeculæ are from the first continuous with the parachordals, and appear to arise as the anterior prolongations of them. There is thus in these animals that which may be regarded as a slight abbreviation of the ancestral history.

At this stage the cranium consists of a membranous investment, with a cartilaginous skeleton consisting of the trabeculæ and basilar plate lodged in its base and supporting the brain; this skeleton is known as the **basis cranii**.

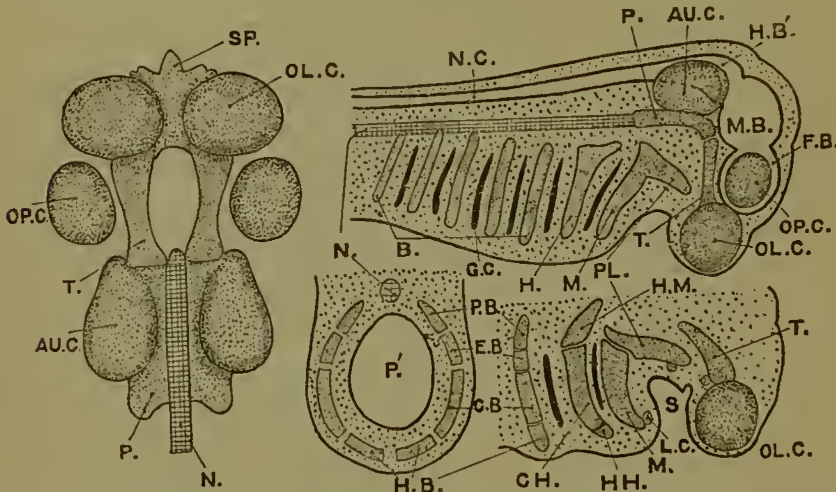

Fig. 15. Development of Dogfish's skull and visceral arches. In part based upon Parker's figures in *Zoological Transactions*, 1877. The left-hand figure represents a dorsal view (from above); the top right-hand figure a lateral view, in which parts have been dissected away to reveal the notochord and central nervous system; the right-hand bottom figure represents the same view of part of the top figure, but at a later stage: the central figure represents a transverse section through the region of the branchial bars. The whole is slightly diagrammatically represented. AU.C = auditory capsule; B = branchial bars; CH = cerato-hyal segment of hyoid arch; C.B = cerato-branchial segment of branchial arch; E.B = epibranchial segment of same; F.B = fore-brain; G.C = gill-cleft; H = hyoid arch; HH = hypo-hyal segment of hyoid arch; H.B' = hind-brain; H.B = hypo-branchial segment of branchial arch; H.M = hyo-mandibular segment of hyoid arch; L.C = labial cartilage; M = mandibular arch in upper figure and Meckelian cartilage in lower one; M.B = mid-brain; N = notochord; N.C = nerve cord; OP.C = optic capsule; OL.C = olfactory capsule; P = parachordial cartilages; P' = pharynx; PL = palato-pterygoid segment of mandibular arch; P.B = pharyngo-branchial segment of branchial arch; S = stomodæum; SP = internasal plate of ethmoid cartilage; T = trabeculæ cranii. The openly dotted portions between the cartilages represent mesoblast.

Very early in development, the mesoblast surrounding the auditory vesicles and the olfactory sacs forms around them definite capsules, in which, later, cartilage is developed; thus are formed the **auditory** and **olfactory capsules** (Fig. 15, AU. C & OL. C, and Fig. 16, A) respectively. The same holds true of the sclerotic of the eye, which forms the **optic capsule** (Fig. 15, OP. C), but which, as we shall see, though it profoundly modifies the skull in the region in which it lies,

does not become merged with that, but remains quite free throughout life; its outer wall is not cartilaginous, but is clear and transparent, and forms the cornea.

The olfactory or nasal capsules are developed immediately in front of the trabeculæ cranii, the optic capsules on either side of the fore-brain, and the auditory capsules on either side of the mid- and hind-brains.

The next stage in development is the formation of the side walls of the brain-case and the hinder part of the roof. This is brought about by an upward growth of the basilar plate behind the auditory capsules, which gives rise ultimately, since the growth is very slow, to a cartilaginous ring investing the hind-brain, and known as the **occipital ring**. In front of it the edges of the basilar plate also grow upwards and become merged with the cartilaginous auditory capsules, while above, the occipital ring grows forwards between the two capsules to form a roof for that part of the cranium. In the case of the rabbit this forward growth does not occur, and the roof in front of the occipital ring remains membranous until the formation of the membrane bones.

The anterior portion of the brain-case, i.e. the orbital and nasal regions, are similarly formed by the upgrowth of the outer edges of the trabeculæ cranii, preceding which, however, these grow forward into the nasal region to form a flat plate of cartilage, the **ethmoidal plate**, the anterior continuation and termination of which is called the **internasal** plate (Fig. 15, SP). In the orbital region, i. e. to the inner side of the eyes, between them and the brain, the trabeculæ grow up on either side to form an **orbito-sphenoidal region** or **plate**, which, in front of the eyes, turns inwards, and more or less separates the brain from the olfactory sacs; this portion of the side wall, i.e. that forming the anterior limits of the brain-case, is called the **lateral ethmoid region**, and it is always pierced for the passage of the olfactory nerves. Behind the eyes, between them and the auditory capsules, the trabeculæ grow up on either side and form the **alisphenoidal region** or **plates**. The upgrowth of the lateral ethmoid, orbito-sphenoid, and alisphenoid regions is a continuous and common one, and these regions are really only localized portions of a single cartilage. In the frog the **orbito-sphenoidal region** arises independently by the formation of a plate of cartilage in the side wall of the membranous case, which, however, soon grows downwards and fuses with the trabeculæ. From the internasal plate an **internasal**

septum grows up, and to its sides the olfactory capsules become attached. The cartilaginous walls, which grow dorsalwards from the trabeculæ, extend inwards over the brain, to form a more or less complete roof; in the dogfish it is not quite complete, since a small part just behind the olfactory capsules, called the **anterior fontanelle**, remains membranous throughout life. The roof is completed in the frog; but in the rabbit, with the exception of the occipital region, cartilage is not formed in the cranial roof, which remains membranous until the formation of the bones.

The Visceral or Branchial Skeleton.

This arises (Fig. 15, B, H, & M) as a series of cartilaginous bars in the mesoblast on either side of the pharynx. In the dogfish there are seven, in the frog six, and in the rabbit five of these bars, of which the most anterior is called the **mandibular arch** (Fig. 15, M), the next the **hyoid arch** (H), and the hinder ones **branchial arches** (B). There are reasons for believing that, in the ancestors of Vertebrates, all these arches once subserved the purpose of supporting gills; and among one of these reasons there may be mentioned that, in the dogfish, a vestigial gill-cleft, i.e. the **spiracle**, exists, and is situated between the hyoid and mandibular arches. But in all jaw-bearing Vertebrates the two anterior arches have become adapted in a remarkable manner to functions totally distinct from those which they primitively served; while in the higher Vertebrates the branchial arches have become, or rather they become in adult life, in part transformed to other uses, and in part they disappear.

Mandibular and Hyoid Arches. These arches depart less from their primitive relations in the dogfish, and most in the rabbit. In the dogfish the mandibular and hyoid arches very early send out (Fig. 15, PL) an anteriorly directed dorsal process from their proximal ends (the end towards the cranium), while the mandibular arch in addition also sends back a very small dorso-posterior process. The anterior process of the mandibular arch is called the **pterygo-quadrate, palato-quadrate**, or **palato-pterygoid bar** (Fig. 15, PL); the smaller posterior process is called the **meta-pterygoid process**, and the ventral end of the cartilage is called the **Meckelian cartilage** (M). The upper portion of the hyoid arch and its anterior process is the **hyo-mandibular** (H.M). At a later stage (Fig. 15, PL, in lower right-hand figure) the palato-quadrate bar becomes segmented off from the

Meckelian cartilage; the former grows forward in front of the mouth and forms the upper jaw, while the latter, situated behind the mouth, by a forward rotation of its ventral end, forms the lower jaw. At their posterior ends these two cartilages articulate with one another. The posterior end of the palato-quadrate bar is enlarged and corresponds to the quadrate region of other Vertebrates. The hyoid arch similarly becomes segmented into two portions, an upper **hyo-mandibular** (H.M) articulated with the cranium beneath the auditory capsule, and a lower **cerato-hyal** (CH) which is connected ventrally with its fellow of the other side by a median **basi-hyal** (HH); originally this latter is composed of two pieces, the **hypo-hyals** (HH), which subsequently fuse and form a basi-hyal.

From the meta-pterygoid process of the palato-quadrate bar (Fig. 17, PRE.L) a ligament passes upwards and becomes attached to the cranium just in front of the auditory capsule; this is known as the **meta-pterygoid** or **prespiracular ligament**. It is supplemented by another which passes from the bar to an attachment at the front of the orbital region of the skull, and is called the **ethmo-palatine ligament** (ETH.PAL.L). These ligaments, however, are comparatively weak, and the main support of the mandibular arch is upon the hyoid arch, by means of two strong ligaments; one, the **symplectic ligament** (Fig. 17, SYM.L), unites the posterior end of the palato-quadrate with the antero-ventral extremity of the hyo-mandibular, and the other, the **mandibulo-hyoid** ligament (M.H.L), attaches the mandible to the cerato-hyal. The mandibular arch is, therefore, not directly articulated to the cranium, but is supported by the hyoid arch; skulls in which this is the case are distinguished, as **hyostylic**, from those, such as the frog's, in which the mandibular arch is directly articulated with the base of the cranium, or **autostylic**.

The simple changes produced by the growth of processes and their segmentation from the body of the cartilage from which they arose, together with a slight alteration in their position, which have been described above, convert the early condition into that of the adult, and we shall not further describe these two arches.

In the frog's tadpole (Fig. 16, A & B), the changes which take place are more complex, and are in some measure due to the fact that a skeleton has to be formed for the temporary horny jaws, which are later replaced by permanent ones. The mandibular arch (Q) is at first a continuous transversely arranged curved band of cartilage, lying in the floor of the mouth near its anterior end, and is from the first

fused with the trabeculæ cranii (T) by its dorsal extremities. A little later it becomes divided on each side into three portions: a small anterior segment, which later fuses with its fellow of the other side and forms the skeleton of the hinder lip of the horny jaw, and is called the **lower labial cartilage** (Fig. 16, L); a small middle segment, or **Meckel's cartilage** (MC), which later forms the basis of the permanent lower jaw; and a larger hinder quadrate segment, the **suspensorium** (Q), which becomes the **quadrate** of the adult skull, and that is from the beginning continuous with the base of the skull by an **otic process** (Fig. 16, B). From the inner side of the quadrate, on either side of the skull, there passes inwards to the anterior end of the trabeculæ a broad plate of cartilage, the **palato-quadrate bar** (Fig. 16, B), which by its elongation later causes the quadrate (Q) to rotate backwards until it assumes the *backward* inclination of the adult skull. This backward inclination characterizes the skull of the tailless Amphibians and distinguishes it from that of the tailed ones (salamanders, newts, &c.), in which the quadrate retains its primitive position and inclines *forwards*. The Meckelian cartilage (MC) articulates with the distal (ventral) extremity of the quadrate, and since the palato-quadrate portion of the mandibular arch is fused with the skull, the skull is of the **autostylic** type as distinguished from that of the dogfish, which is hyostylic (ante, p. 59). In consequence of this, the fate of the hyoid arch in the frog is different from that in the dogfish, where, in addition to supporting a half gill, it also supports the mandibular arch. In the frog, the hyoid arch (Fig. 16, CH) lies behind the mandibular and is at first very thin and narrow, but it very rapidly thickens and widens to form a lozenge-shaped plate

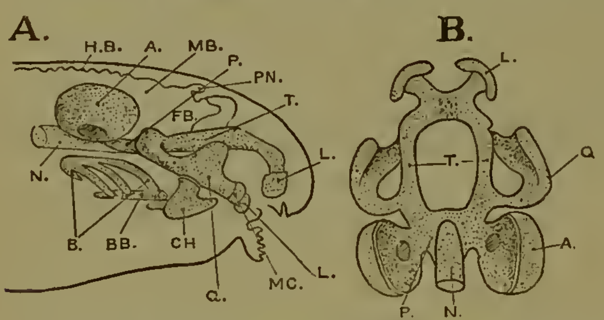

FIG. 16. The chondro-cranium of the Frog's tadpole. A. Side view. B. Dorsal view. (From Marshall's Vertebrate Embryology.) A = auditory capsule; B = branchial arches; BB = basi-branchial; CH = cerato-hyal; FB = fore-brain; H.B = hind-brain; L = labial cartilages; MB = mid-brain; MC = Meckel's cartilage; N = notochord; P = parachordal cartilage; PN = pineal body; Q = quadrate; T = trabeculæ. The palato-quadrate cartilage is not lettered, but it can be seen in B as the bar extending from Q forwards to the anterior end of T; the otic process is the bar at the other end of Q and just in front of A, and reaching inwards to the posterior end of T with which it is fused.

of cartilage, which articulates by its antero-dorsal angle with the suspensorium (quadrate) about its middle. At first the plates of either side are separated ventrally, but they soon become connected by a median **basi-hyal** which grows back posteriorly as a **uro-hyal process**. The lozenge-shaped cartilage above mentioned does not, as in the dogfish, undergo segmentation into a dorsal hyo-mandibular and a ventral cerato-hyal. Indeed, it is doubtful whether in the frog there is any element which can be compared to the hyo-mandibular of fishes, unless the columella auris, on account of the similarity of its nerve supply, can be regarded as its homologue. On the other hand, the early ligamentous connexion of the upper portion of the hyoid with the quadrate (suspensorium) would seem to indicate that this portion of the primitive hyoid is the hyo-mandibular which had not separated off from the remaining portion (cerato-hyal). But whichever view we accept as to the hyo-mandibular, there is no doubt that in its relations and position the main portion of the primitive hyoid plate represents the **cerato-hyal** of fishes, and by that name it is known.

During the remaining period of development, the cerato-hyal (CH) elongates considerably and becomes bent into an S-shaped rod; its ventral end fuses with the basi-hyal, and that in turn with the median basal plates of the branchial arches behind, to form a **hyo-branchial plate** (Fig. 50, HY.PL). At this stage, therefore, there is a flat, broad median plate with five arches (Fig. 16, A) arising from it on either side, i. e. the anterior pair of cerato-hyals (CH), and behind these, the four pairs of branchial arches (B). Very soon after this, the cerato-hyal grows up and expanding somewhat at its dorsal extremity, forms the **stylo-hyal (anterior cornu)** (Fig. 50, AN.C, and Fig. 18, ST. HY), and becomes merged with the lower border of the periotic (auditory) cartilage. The first and second branchial arches for the most part disappear, except that the ventral part of the first may form the anterior process of the hyoid, and the basal portion of the third remains as a pair of pointed cartilaginous processes from the posterior angles of the hyo-branchial plate and as the arytenoid cartilages of the thyroid (Fig. 27, ARY); while the fourth branchial arch (or rather its basal portion) persists as the **thyro-hyals (posterior cornu)**—a pair of ossified processes projecting from the curved hinder border of the hyo-branchial plate (Fig. 50, POS.C)—and as the cricoid cartilages of the thyroid.

In the embryo of the mammal [1], though the most remarkable meta-

[1] The embryo of the pig is here taken since the development of its skull is better known than that of the rabbit.

morphosis takes place, yet the processes connected with the changes of these two arches (mandibular and hyoid) are not quite so complex as those in the frog. The palato-quadrate bar is from the very beginning distinct from the mandibular arch. The latter consists of an elongated cartilaginous bar (Meckelian cartilage), stretching forwards along either side of the mouth to its anterior end; dorsally it is expanded to form the quadrate portion. Later in development the quadrate portion assumes a peculiar form, likened to that of a hammer, and becoming constricted off and ossifying forms one of the bones (**malleus**) of the middle ear. Behind this, the dorsal part of the hyoid arch becomes segmented off to form the **incus**, another of the bones (auditory ossicles) of the middle ear. The anterior portion of the hyoid persists permanently as the anterior cornu of the hyoid bone. The third of the auditory ossicles, the **stapes**, is segmented off from the fenestra ovalis, which is one of the two foramina placing the internal ear in communication with the cavity of the middle ear.

Development of Branchial Arches. The developmental changes of these is very simple. Primitively each branchial arch forms a curved band of cartilage embracing the pharynx and meeting its fellow of the other side in the middle line (Fig. 15, central figure). This simple band of cartilage becomes segmented into four on either side (Fig. 15, the central figure): a dorsal **pharyngo-branchial segment** (Fig. 17, PH-BR, & Fig. 15, P.B), followed ventrally and in order by **epi-branchial** (Fig. 15, E.B., Fig. 17, EP.B), **cerato-branchial** (Fig. 15, C.B., Fig. 17, CER-BR) and **hypo-branchial** (Fig. 15, H.B) **segments**, the latter lying immediately on either side of the middle line. In some cases, the hypo-branchials of either side, of one or more of the arches, unite to form a median **basi-branchial** (Fig. 17, BB).

In fishes, the branchial arches remain throughout life and support a gill on either face, while their fate in the frog has already been described (ante, p. 61). In the mammal (rabbit) the basi-branchial of the first branchial arch unites with the basi-hyal to form the body of the hyoid, while the lower portion of the first branchial arch remains as the posterior cornu of the hyoid bone, its anterior cornu being formed by the cerato-hyal and stylo-hyal, the latter usually becoming ossified and fused with the periotic (auditory) capsule to form the **styloid process (stylo-mastoid process)** (Fig. 19, S-M).

The second and third branchial arches undergo a certain amount

of retrogression in the mammal, but part of them give rise to the thyroid cartilage (Adam's apple) of the larynx, while the third, in addition, probably also forms the **arytenoid** cartilage of the same organ. The ventral portion of the fourth branchial arch probably gives rise to the most posterior cartilage of the larynx, i. e. the **cricoid.**

THE METAMORPHOSIS OF THE VISCERAL ARCHES.

	Dogfish.	Frog.	Rabbit.
1st or Mandibular arch.	Becomes the upper and lower jaws.	Becomes the basis of the upper and lower jaws and forms the labial cartilages of tadpole. Quadrate portion fuses with auditory capsule and forms a suspensorium for lower jaw (**auto-stylic skull**).	The basis of upper jaw (palato-quadrate) distinct from beginning from the basis of lower jaw (Meckel's cartilage). Quadrate portion becomes the malleus of the auditory ossicles.
2nd or Hyoidean arch.	Forms a hyo-mandibular, supports the mandibular arch (**hyo-stylic skull**), and bears a half gill.	Hyo-mandibular questionably present; the cerato-hyal fuses with basi-hyal and this with basi-branchials to form the body and anterior cornu of the hyoid bone. Does not support the mandibular arch.	Dorsal portion probably becomes the incus of auditory ossicles and perhaps the styloid process of skull. The ventral portion becomes the anterior cornu, and in part the body of hyoid bone.
3rd or First branchial arch.	Persists throughout life as a gill-supporting arch.	Basi-branchial forms part of body of hyoid, and the ventral portion of arch forms the anterior process of that, the dorsal portion retrogressing.	Basi-branchial fuses with basi-hyal to form the body of hyoid; the ventral part of arch remains as the posterior cornu of that.
4th or Second branchial arch.	Persists throughout life as a gill-supporting arch.	Basi-branchial forms part of the body of hyoid: the dorsal portion of arch retrogresses.	Takes part in the formation of the thyroid cartilage.

THE METAMORPHOSIS OF THE VISCERAL ARCHES (*continued*).

	Dogfish.	Frog.	Rabbit.
5th or Third branchial arch.	Persists throughout life as a gill-supporting arch.	Probably forms the posterior process of hyoid and arytenoid cartilage. Basi-branchial forms part of body of hyoid.	Takes part in the formation of the thyroid cartilage, and also probably the arytenoid cartilage.
6th or Fourth branchial arch.	Persists throughout life as a gill-supporting arch.	Basi-branchial forms part of the body of the hyoid. Ventral portion of arch gives rise to the posterior cornu and probably to the cricoid cartilage.	Gives rise probably to the cricoid cartilage.

THE ADULT SKULL.

Dogfish. The fully formed skull of the dogfish (Fig. 17) consists of a cartilaginous box or **cranium** enclosing the brain, of three pairs of sense capsules, i.e. the **olfactory** or **nasal** (OLF.CAP), the **auditory** or **otic** (AUD.CAP), and the **optic capsules** or **sacs**; the two first named early become fused with the cranium, while the last-named one forms the cartilaginous investment of the eyeball known as the **sclerotic.** Connected more or less directly with the skull is a series of arches, the **visceral** or **branchial arches**, which have already been considered.

The roof of the cranium is not complete, since it is partially open by means of a large oval aperture, the **anterior fontanelle**; in the fresh skull, however, this is closed by membrane, and beneath it the pineal body (or middle eye) lies. The olfactory capsules are large oval cartilaginous cups with their open ends downwards and separated in the middle line from each other by the internasal septum (ante, pp. 57). The aperture of each sac is partially closed by a pair of **nasal cartilages** (Fig. 17, LA.C) which grow backwards over the aperture from its anterior margin; from the front of the capsules there project three processes, the **lateral** and **median processes** of the **rostrum** (R.P).

The auditory capsules (AUD.CAP) are large projections at the hinder end of the skull lodging the auditory apparatus; they communicate with the exterior only through a tubular canal, the **aqueductus**

vestibuli, which opens on either side in a median depression, the **posterior fontanelle**, situated in the roof of the cranium between the capsules.

Between the olfactory and auditory capsules, on either side, there is a deep concavity, in which is lodged the **optic capsule**; this is known as the **orbit** (Fig. 17, OR), and it is bounded above by a prominent **supra-orbital ridge** and below by a **sub-orbital ridge**. In its inner lateral wall are several foramina for the exit of cranial nerves, of which the optic foramen, conveying the optic nerve, is the largest, and is situated near the middle and close to the ventral border (FOR. 2nd); vertically above this foramen is a very small one for the passage of the

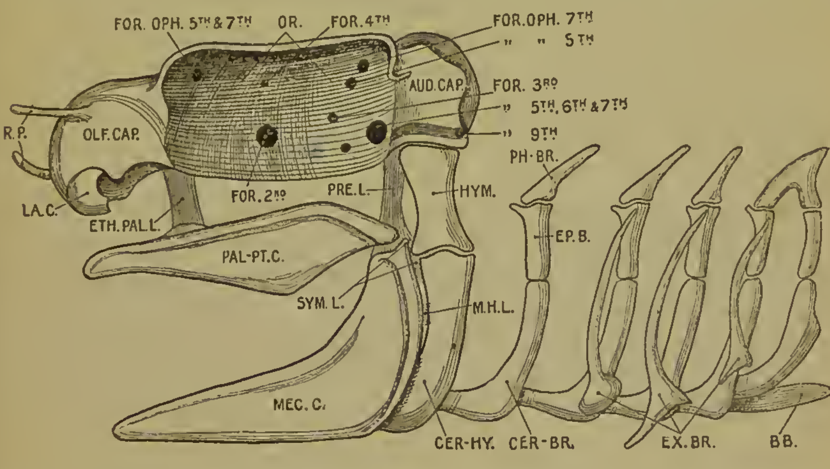

FIG. 17. Lateral view of the skull and visceral arches of Dogfish (*Scyllium*). AUD.CAP = auditory capsule; BB = basi-brancbial cartilage; CER-BR = cerato-branchial cartilages; CER-HY = cerato-hyoid cartilage; EP.B = epi-branchial cartilages; ETH.PAL.L = ethmo-palatine ligament; EX.BR = extra-branchial cartilages; FOR. 2nd, 3rd, 4th, 5th, 6th, 7tb, & 9th = foramina of exit for the different cranial nerves; HYM = hyo-mandibular; LA.C = nasal (one of the labials) cartilage; MEC.C = Meckel's cartilage; M.H.L = mandibulo-hyoid ligament; OLF.CAP = olfactory capsule; OR = orbit; PAL-PT.C = palato-pterygoid cartilage; PH.BR = pharyngo-branchial cartilages; PRE.L = prespiracular ligament; R.P = rostral processes of olfactory capsules; SYM.L = symplectic ligament.

fourth nerve (FOR. 4th), and a little way behind this and slightly below it is the small aperture through which passes the third nerve (FOR. 3rd). At the posterior end of the orbit and in its lower angle is a foramen as large as that of the optic, through which pass the main trunks of the fifth and seventh nerves and also the sixth (FOR. 5th, 6th & 7th). The **inter-orbital canal** is a blood channel placing the orbits, which are themselves blood sinuses, in connexion with each other; its opening on either side is situated a little below and in front of that just described. Situated in the dorso-posterior corner of the orbit are two other

apertures, the posterior and upper of which transmits the ophthalmic branch of the seventh nerve (FOR.OPH. 7th), and the anterior and lower one the corresponding branch of the fifth nerve (FOR.OPH. 5th). These two branches unite in the orbit, and travel forward along its lateral wall to leave it by a foramen in its upper anterior angle (FOR.OPH. 5th & 7th). At the posterior end of the skull there is a large median aperture, the **foramen magnum**, through which the spinal cord passes, and on either side and slightly below this are the two condyles for articulation with the first vertebra. Below and to the inner side of the auditory capsule, between it and the condyle, is a pit-like depression, at the bottom of which is the aperture of exit for the tenth or vagus nerve. Running beneath the auditory capsule is a deep groove, the **post-orbital groove**, which extends from the postero-inferior angle of the orbit to the hinder end of the auditory capsule, and in life conveys the blood from the orbit to the anterior cardinal vein ; at its posterior end, the aperture of exit of the ninth or glosso-pharyngeal nerve (FOR. 9th) can be seen.

The visceral skeleton has already been described, and there only remains a description of the nature of the **extra-branchial** and **labial cartilages**. The latter are five in number, and are related to the anterior and ventral faces of the olfactory sac and to the palato-quadrate and angle of the jaw ; the former (EX.BR) are elongated cartilages lying on the outside of the second, third, and fourth branchial arches. They probably represent remains of the basket-like branchial skeleton and labial cartilages of the lamprey.

Frog. The skull of the frog consists of a primarycartilaginous one (Fig. 18, D), the **chondro-cranium**, and an external one moulded in bone upon and in part within this, the **osseous cranium** (Fig. 18, A & B).

The chondro-cranium. In its fundamental form this resembles that of the dogfish, but differs from it in that the orbital cavity is bounded ventro-laterally by the palato-pterygoid cartilage (D, PT), and that some portions of it become ossified to form definite bony tracts.

It consists of a tubular brain-case, wider posteriorly and open above by a large oval foramen, the **frontal fontanelle**, and behind this two smaller ones, which are filled in during life by a connective tissue membrane ; the latter are situated just to the inner side of the auditory capsules. Anteriorly a ring-like bone, the **sphenethmoid** (SP), is formed in it, and beyond this there are the two **olfactory capsules** fused together (NAS.CAP), with their peculiar cartilaginous processes

and labial cartilages; posteriorly, at their junction with the sphenethmoid, they send off on either side a transverse bar of cartilage which becomes continuous (E.P) with that of the pterygoid region (Fig. 18, D).

At the hinder end of the skull, and situated on either side, are the **auditory capsules** (AUD), confluent with the brain-case, and containing the ossification of the **pro-otic bone** (P-O) in their anterior walls, and which also extend upwards and downwards to their dorsal and ventral walls. On either side of the foramen magnum there is another ossification (EX), extending to the dorsal and ventral walls, and antero-laterally almost meeting the pro-otic; these are the ossifications of the **exoccipital bones.** The **suspensorium** or **quadrate** (QU) is in part fused with the brain-case and in part articulated with it; it passes downwards, outwards, and backwards, and its posterior end forms an articulation for the lower jaw, while its anterior end is divided into two arms, one of which, its **dorsal crus** or **otic process** (O.P), is merged with the auditory capsule and the anterior one, its **pedicel** (PED), articulates with that at the outer side of the fenestra ovalis. It will be seen from this description that the only bones which are formed in cartilage (**cartilage bones**) in the chondro-cranium of the frog, are the paired **exoccipitals**, the paired **pro-otics**, and the **girdle bone** or **sphenethmoid**; so that, even in the adult frog, a considerable portion of the primitive skull remains cartilaginous.

The osseous skull. This consists of a series of membrane bones, formed independently of the chondro-cranium, though later it becomes grafted upon it. The bones of which it is composed are formed in a loose connective tissue membrane that invests the cartilaginous skull.

One of the first of the membrane bones to develop is the **parasphenoid** (Fig. 18, B, PAR), a dagger-shaped bone lying along the base of the skull, the transverse bar or handle of which supports the auditory capsules. On the roof of the skull, two pairs of bones next develop, the posterior of which are known as the **parietal** and the anterior as the **frontals**; the former covers the parietal (smaller) fontanelles and lie for the most part between the auditory capsules, while the latter covers the frontal (larger) fontanelle and lie between the orbits. Very soon after their formation they fuse together, to form a single bone on either side, the **fronto-parietal** (F.P). In front of these, the olfactory capsules are partially covered by the paired triangular **nasal** bones

(N), anteriorly to which the rounded summit of the upper jaw is completed by the two dentulous **premaxillæ** (PM). Right and left of these are the slightly bent denticulate **maxillæ** (M), continued backwards by fusion with a very slender bone, the **quadrato-jugal** (J), which posteriorly comes in contact with the quadrate cartilage and **squamosal** (SQ). The latter is a T-shaped bone, with the longer arm

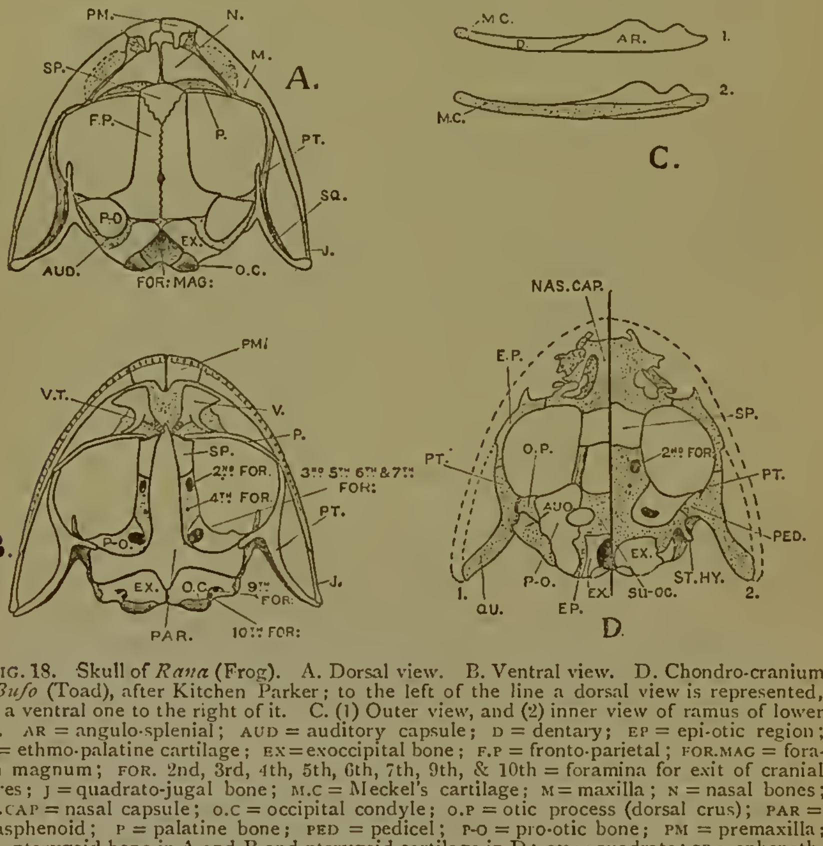

FIG. 18. Skull of *Rana* (Frog). A. Dorsal view. B. Ventral view. D. Chondro-cranium of *Bufo* (Toad), after Kitchen Parker; to the left of the line a dorsal view is represented, and a ventral one to the right of it. C. (1) Outer view, and (2) inner view of ramus of lower jaw. AR = angulo-splenial; AUD = auditory capsule; D = dentary; EP = epi-otic region; E.P = ethmo-palatine cartilage; EX = exoccipital bone; F.P = fronto-parietal; FOR.MAG = foramen magnum; FOR. 2nd, 3rd, 4th, 5th, 6th, 7th, 9th, & 10th = foramina for exit of cranial nerves; J = quadrato-jugal bone; M.C = Meckel's cartilage; M = maxilla; N = nasal bones; NAS.CAP = nasal capsule; O.C = occipital condyle; O.P = otic process (dorsal crus); PAR = parasphenoid; P = palatine bone; PED = pedicel; P-O = pro-otic bone; PM = premaxilla; PT = pterygoid bone in A and B and pterygoid cartilage in D; QU = quadrate; SP = sphenethmoid; SQ = squamosal; SU-OC = supra-occipital; ST.HY = stylo-hyal; V = vomer bone; V.T = vomerine teeth. The fenestra ovalis is hidden from view by the stylo-hyal (ST.HY); it lies just below that in the position of the sketch.

passing down over the dorsal surface of the suspensorium (quadrate) which it completely hides; the shorter arm passes from the outer edge of the pro-otic towards the **pterygoid** bone (PT, A & B).

On the under (ventral) surface of the skull, beneath the floor of the nasal sacs, a pair of denticulate triangular bones may be seen, with their apices directed inwards and resting on the front (anterior) edge

of the sphenethmoids; these are the **vomers** (V & V.T) which, with the other two bones to be next described, do not appear until the close of the metamorphosis (until the tadpole has become a frog). The **palatines** (P) are paired bones, transversely arranged and passing from the anterior end of the girdle bone outwards to the maxillæ. The **pterygoids** (PT, A & B) are paired bones, each consisting of three arms, of which the anterior and longest runs forward under the palato-pterygoid cartilage[1] and meets the outer extremity of the palatine bone at its junction with the maxilla; the inner and median arm passes to the pro-otic and becomes connected with it by a short cartilaginous process, while the posterior arm is grooved and lies upon the under surface of the suspensorium (quadrate).

The foramina through which the cranial nerves leave the skull are as follows:—

The 1st pair or **olfactory** nerve passes through the two canals formed by the presence of a median septum in the anterior end of the sphenethmoid.

The 2nd pair or **optic** nerve passes through the optic foramen (2nd FOR), a large aperture in the cartilaginous inner wall of the orbit.

The 3rd pair or **oculo-motor** nerve passes out with the 5th, 6th, and 7th nerves.

The 4th pair or **pathetic** nerve pierces the cartilaginous wall between the aperture of the 2nd and 3rd nerves (4th FOR).

The 5th pair or **trigeminal** nerve passes out just in front of the auditory capsule, in a foramen cut out in the inner hinder border of the pro-otic.

The 6th pair or **abducens** passes out with the last nerve.

The 7th pair or **facial** nerve leaves the skull with the 5th and 6th nerves (3rd, 5th, 6th, & 7th FOR).

The 8th pair or **auditory** nerve passes out through a foramen in the inner wall of the auditory sac.

The 9th or **glosso-pharyngeal** and the 10th or **vagus** nerves pass out through two foramina very close together, and pierce the exoccipital bone to the outer side of the occipital condyle (9th FOR & 10th FOR).

The lower jaw or **mandible** (Fig. 18, C) is composed of two portions or **rami**, united in the middle line distally and articulating

[1] The student must not forget that the terms 'palato-pterygoid,' 'palato-quadrate,' and 'quadrato-pterygoid' are interchangeable.

with the quadrate proximally. Each ramus consists of two membrane bones, the **dentary** (D) and **angulosplenial** (AR), arranged upon the surface of Meckel's cartilage (M.C). Proximally Meckel's cartilage is enlarged to form an articulation which works on the quadrate, and distally beyond the extremity of the dentary it is ossified as a small **mento-meckelian** cartilage bone.

The hyoid. This consists of a cartilaginous plate, the body of the hyoid (Fig. 50, BAS), from which there arises anteriorly a pair of long S-shaped processes (AN.C) which serve to attach the hyoid to the skull; they are the **anterior cornu.** Just behind them are a pair of very short and blunt processes, which probably represent the last traces of the 1st branchial arch. At the posterior end are another two pair of processes, the hinder of which, the **posterior cornu** (POS.C), are ossified. (Cp. ante, p. 60.)

TABULATION OF THE CRANIAL BONES.

Cartilage bones.	Membrane bones.	
	Dorsal surface.	*Ventral surface.*
Pro-otic (*paired*).	Fronto-parietals (*paired*).	Parasphenoid (*unpaired*).
Exoccipital (*paired*).	Nasals (*paired*).	Palatines (*paired*).
Sphenethmoid.	Squamosals (*paired*).	Vomers (*paired* and *dentulous*).
		Pterygoids (*paired*).
Of lower jaw.	*Of lower jaw.*	Maxillæ (*paired* and *dentigerous*).
Mento-meckelian.	Angulo-splenial.	Premaxillæ (*paired* and *dentigerous*).
	Dentary.	Quadrato-jugals (*paired*).

Dog. In the skull of the dog several important features of difference exist between it and those already described. The parasphenoid bone of the frog and bony fishes is no longer represented; the basal portion (Fig. 20) of the chondro-cranium ossifies at several centres to form the **presphenoid** (PR), **basi-sphenoid** (B-S), and **basi-occipital** (B-O) bones, and as these form a rigid base for the adult skull, the presence of a parasphenoid is thereby rendered unnecessary. The **squamosal** bone (Fig. 19, SQ), which in bony fishes, amphibians, and reptiles is completely outside the brain-case, in the dog and all other mammals not only takes part in the formation of that, being a constituent bone of the lateral walls, but the **zygomatic process** arising from it forms the articulation for the lower jaw, the quadrate

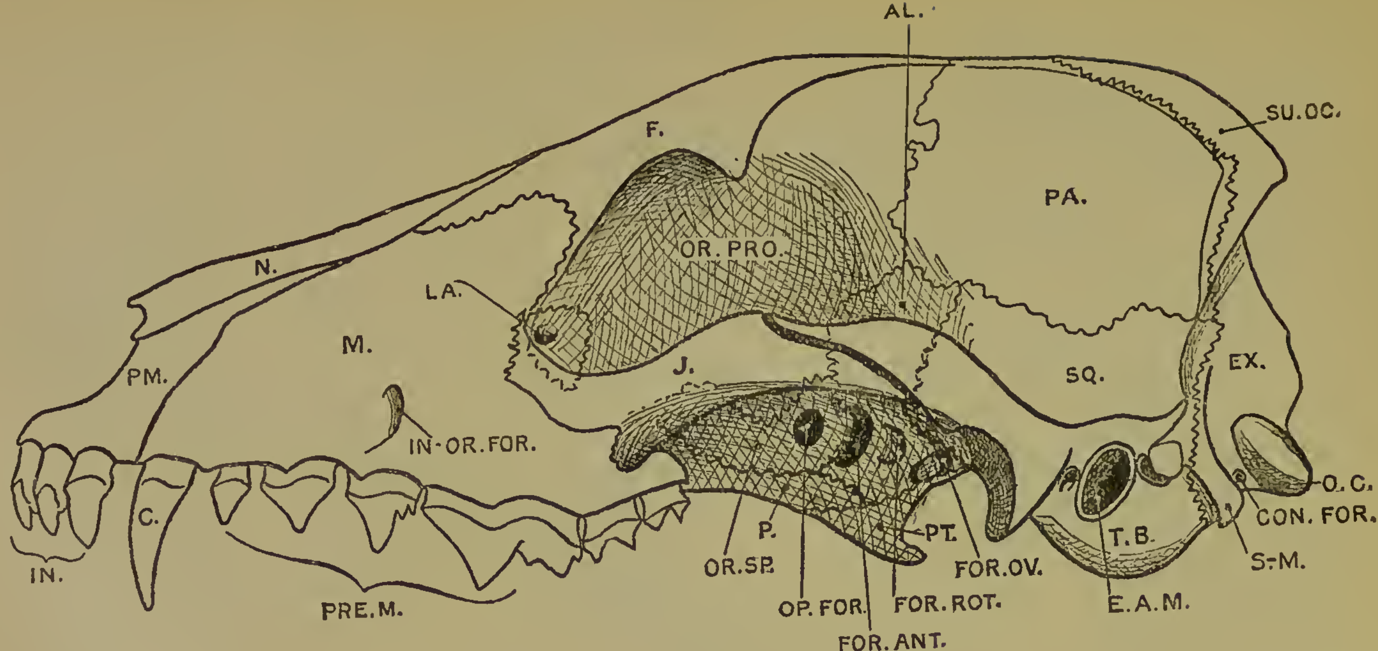

FIG. 19. Lateral view of Dog's skull. AL = alisphenoid bone; C = canine; CON.FOR = condylar foramen; EX = exoccipital; E.A.M = external auditory meatus: the internal auditory meatus is the small aperture just in front, and the stylo-mastoid foramen, a larger one just behind E.A.M; F = frontal bone; IN = incisor teeth; IN-OR.FOR = infra-orbital foramen; J = jugal bone; LA = lachrymal bone; M = maxilla; N = nasal; OR.SP = orbito-sphenoid; OP.FOR = optic foramen; O.C = occipital condyle; OR.PRO = orbital process of frontal bone; P = palatine; PT = pterygoid; PA = parietal; PRE.M = premolar teeth: the two molar teeth are immediately behind them; PM = premaxilla; SU.OC = supra-occipital; SQ = squamosal; S-M = stylo-mastoid process; T.B = tympanic bulla; FOR.ANT = foramen lacerum anterius; FOR.ROT = foramen rotundum; FOR OV = foramen ovale.

having become converted to other uses (ante, p. 62). The squamosal articulation of the lower jaw is not only characteristic, but is diagnostic, of the mammalian skull. As in Amphibia, but unlike that in reptiles and birds, the exoccipitals produce paired condyles. The **cranial cavity** is roofed in by paired **frontals** (Figs. 19 & 21, F), **parietals** (Fig. 19, PA, Fig. 21, P), and an unpaired **inter-parietal** and **supra-occipital** (Fig. 19, SU.OC & Fig. 21, S-A), which in the young animal, and even up to adult life, are united by sutures, that in old age tend to become obliterated by bony fusion.

The auditory capsules are ossified from three centres, the **pro-otic**, **epi-otic**, and **opisthotic**, which early fuse together to form a single bone, the **periotic** (Fig. 20, PER) or **petro-mastoid**. The inner, denser (petrous) portion of this encloses the internal ear, and upon its outer surface are situated the two apertures of that, the **fenestræ rotunda** and **ovalis**. The student must not confuse these with the foramina ovalis and rotundum. The periotic is covered externally by a **tympanic bone** (Figs. 19 & 20, T.B), consisting of a swollen portion, the *tympanic bulla*, which lodges the auditory ossicles, i. e. the **malleus**, **incus**, and **stapes**, and of a tubular portion, the **external auditory meatus** (E.A.M), which in life is closed by the tympanic membrane. The bulla is perforated by a canal, the **Eustachian tube** (Fig. 20, EUS.C), at its antero-inner corner, by which the pharynx and the middle ear are placed in communication.

In front and above the periotic is the **squamosal bone** (Fig. 19, SQ), forming a great portion of the infero-lateral boundary of the cranium, and sending out a very large curved process, the **zygomatic process**, which meeting the **jugal** (J), and in old skulls merging with it, forms an outer arch-like boundary to the orbit; upon the postero-under surface of the zygomatic process, and just at its origin from the squamosal, is a concave articulation for the lower jaw. The **temporal bone** of the human skull represents the fused squamosal, periotic, and tympanic of the dog's.

The **nasal cavity** is roofed in by the paired **nasal bones** (Figs. 19 & 21, N) and the **premaxillæ** (Fig. 19, PM), the latter also surrounding the **naso-palatine canal** in the anterior portion of the nasal floor. The posterior portion of the nasal cavity is bounded by the **cribriform plate** of the **ethmoid bone**, through the numerous openings in which the branches of the olfactory nerves pass out from the brain-case; the cribriform plate separates the cranial and nasal cavities. The

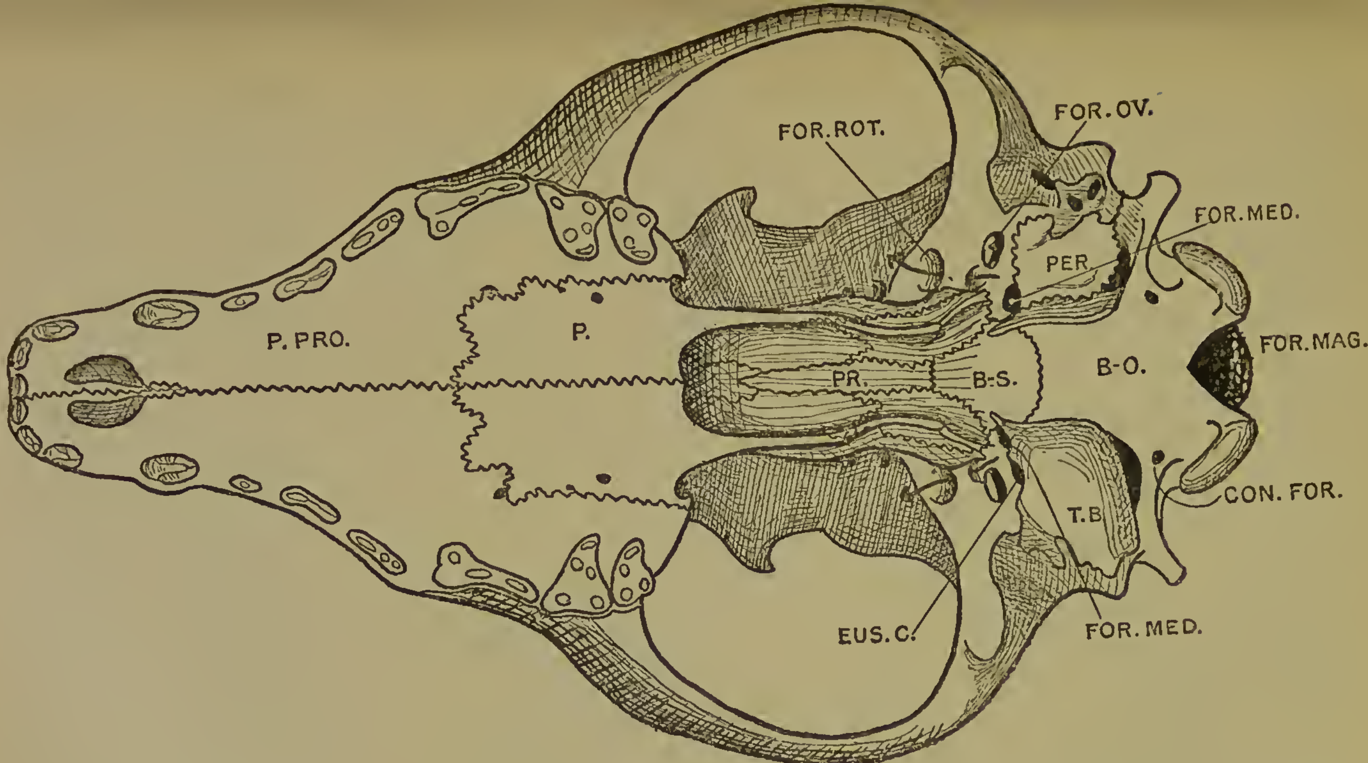

FIG. 20. Ventral view (under surface) of skull of Dog (*Canis domestica*). B-O = basi-occipital; B-S = basi-sphenoid; CON.FOR = condylar foramen; EUS.C = Eustachian tube or canal; P = palatine: the letter is placed upon the palatine process of the palatine, but the bone itself extends back to either side of the presphenoid; PR = presphenoid; PER = periotic; P.PRO = palatine process of maxilla. The pterygoid bones are not lettered, but they articulate with the palatine in front, the presphenoid and basi-sphenoid within, and without they limit the inner-hinder part of the orbit. T.B = tympanic bulla; FOR.MAG = foramen magnum; FOR.MED = foramen medium lacerum basis cranii; FOR.ROT = foramen rotundum; FOR.OV = foramen ovale. On the right-hand side of the skull, the tympanic bulla has been removed in order to show the periotic bone. The foramen lacerum posterius is not lettered, but it is the slit-like aperture lying between the tympanic bulla on the left, or the periotic on the right, and the condylar foramen.

nasal cavity is divided into two chambers by a **nasal septum**, the hinder portion of which becomes ossified to form the **mesethmoid** (Fig. 21, ME); the hinder margin of this is merged with the cribriform plate, and its lower margin is rounded and lies in a deep groove of a median boat-shaped bone, the **vomer** (Fig. 21, V). The cavity of each nasal chamber is further very much subdivided by two scroll-like bones, the **turbinals**, of which the posterior one is fused with the mesethmoid and is called the **ethmo-turbinal**, while the anterior one is merged with the inner surface of the maxilla (MA) and is called the **maxillo-turbinal** (Fig. 21, M-T).

The **hard palate** is constituted by two pairs of processes which meet and fuse in the middle line; the anterior pair, called the **palatine processes** of the maxilla (Fig. 20, P.PRO & Fig. 21, P.MA), are inward plate-like projections of that bone, and the posterior pair (Fig. 20, P) are similar projections of the **palatine bones**. The small **pterygoid bones** (Figs. 19 & 21, PT), which lie behind the palatines, do not take part in the formation of the palate as in ant-eaters and some whales. The hard palate forms the floor of the nasal cavity. Posteriorly, where the palate (P) ends the nasal cavity opens by a very large single aperture, the **internal nostril**, into the roof of the pharynx (Fig. 20); and anteriorly the nasal cavity also opens into the cavity of the mouth by the paired **naso-palatine** openings (Fig. 20).

The orbit of the eye is bounded on its inner surface by the orbital process of the frontal (Fig. 19, OR.PRO & Fig. 21, O.P) and the **orbito-sphenoid** (Fig. 19, OR.SP, Fig. 21, OS); posteriorly by the **alisphenoid** (Fig. 19, AL); anteriorly by the **maxilla** and **lachrymal** (Fig. 19, M & LA), the latter of which is pierced by a canal, the **lachrymal canal**, that places the orbit in communication with the nasal cavity; and outwardly by the **zygomatic arch** formed by the union of the **jugal bone** (Fig. 19, J) and the zygomatic process of the squamosal.

The rami of the **mandible**, unlike that of the frog, are each composed of one membrane bone only, arranged round the primitive Meckel's cartilage, and which essentially corresponds to the **dentary** of the frog.

Segmentation of the Skull. Taking a general survey of the plan of organization of the dog's skull, especially if it be a young specimen longitudinally bisected, it will be observed that it is a tubular structure dilated at one portion, and opening posteriorly by the foramen magnum and anteriorly by the cribriform plate. This tube will be distinctly seen to be composed of three segments, and of a fourth less

obvious one, each of which consists of a basal, a lateral, and a roofing portion; each segment is named in order from behind to before as the **occipital, parietal, frontal,** and **ethmoidal segments**. A transverse

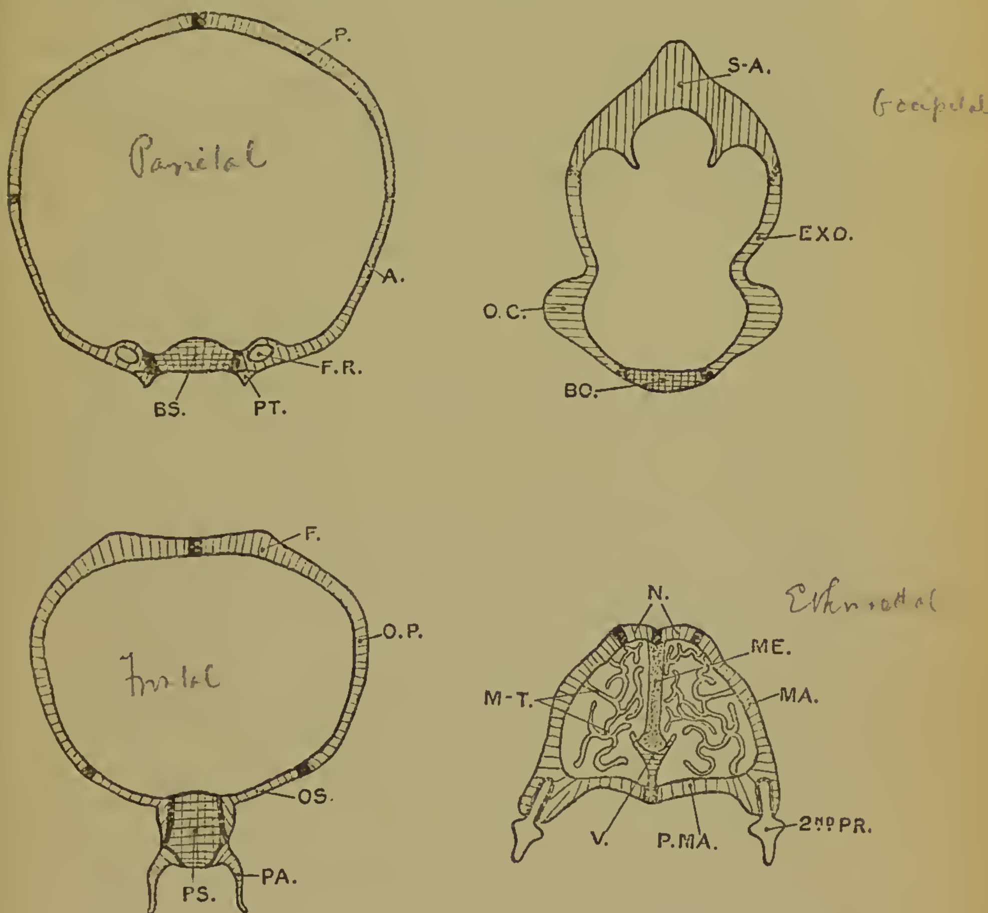

FIG. 21. Four transverse sections through the skull of Dog. Top right-hand figure = section through **occipital segment**; top left-hand figure = section through **parietal segment**; bottom left-hand figure = section through **frontal segment**; and bottom right-hand figure = section through **ethmoidal segment**, somewhat far forward. S-A = supra-occipital; EXO = exoccipital; O.C = occipital condyle; BO = basi-occipital; P = parietal; A = alisphenoid; BS = basi-sphenoid; PT = pterygoid; F.R = foramen rotundum; F = frontal; O.P = orbital process of frontal; OS = orbito-sphenoid; PS = presphenoid; PA = palatine; N = nasal; ME = mesethmoid; MA = maxilla; M-T = maxillo-turbinal; P.MA = palatine process of maxilla; V = vomer; 2nd PR = second premolar.

section of the skull through the occipital region is represented in Fig. 21, in the right-hand top corner, and shows that the base of the segment is formed by the **basi-occipital** (BO), the side walls by the **exoccipitals** (EX.O), and the roof by the **supra-occipital** (S-A). A

similar section (Fig. 21, left-hand top corner), passing through the parietal segment, shows this to be composed of a basal **basi-sphenoid** (BS), of two lateral **alisphenoids** (A), and paired **parietals** (P) roofing it in above. In the same way the frontal segment (Fig. 21) is composed of a **presphenoid** (PS) forming the base, of an **orbito-sphenoid** (OS) forming a part of the side wall on either side, and of paired **frontals** (F) and processes of the frontals (OP) constituting the roof and the superior portion of the side wall. The ethmoid segment is composed of the **nasals** (N) above, the **vomer** (V) below, and the **ethmo-turbinals** laterally.

Studying the organization of the adult skull alone, it appears that each segment is built upon the same plan as the vertebræ, in which the basal bones, i.e. the presphenoid, basi-sphenoid and basi-occipital, correspond to the centra, and the remaining bones to the neural arches. Based upon mistaken homologies of this sort, as Huxley first demonstrated them to be, taken in conjunction with the fact that the skull and vertebral column both pass through a membranous, cartilaginous, and bony stage, and that the primitive notochord extends forward for a certain distance into the base of the skull, the older anatomists, led by Goethe and Oken, and supported by Cuvier and Owen, regarded the brain-case as a structure composed of inflated and modified vertebræ.

The facts of development show, however, that the cranium is never composed of metamerically arranged cartilaginous portions, which is one of the most constant characters of a vertebra; that, if the occipital region be excepted, it develops independently of the notochord, whereas the vertebræ are always developed in close association with that; and that the parietal and frontal bones forming the arch of these segments are membrane and not cartilage bones. Moreover, the origin of the skull from paired trabeculæ and parachordals is quite different to the origin of a vertebra.

On the other hand, the early fusion of the parachordal cartilages and the posterior extremities of the trabeculæ with the anterior end of the notochord seems to indicate that the occipital region, at any rate, may represent, either in whole or in part, a modified first vertebra. It is possible, if not probable, that this connexion of parachordals and trabeculæ is a secondary one and therefore of no significance. The vertebral origin of the occipital region is further supported by the fact that in certain bony fishes, i.e. cod and haddock, the first vertebra is in the course of becoming confluent with the occipital region of the

skull, while in certain other fishes the two first vertebræ have actually become fused with it. Moreover, a comparison of the hypoglossal nerve of the frog with that of the rabbit also leads to the same conclusion, for in the former animal this nerve is the first spinal, but in the latter the last cranial, thus suggesting that the last cranial nerve of the mammal is the first spinal of the amphibian which has undergone this change as a result of the incorporation of the anterior vertebræ. Such a conclusion becomes a demonstrated fact when, in the course of the development of this nerve in mammals, it is known that it arises not by a single, but by a double root, i.e. a dorsal ganglionated one and a ventral unganglionated one, which unite to form the single nerve trunk, an arrangement that is characteristic of spinal nerves; later in development the dorsal root disappears, leaving the hypoglossal with the apparent relations of a cranial nerve.

The theory of the segmentation of the skull, therefore, like so many other theories, is now dead and buried; but it must not be thought that, because it was false, it was necessarily a useless incumbrance to science; for, as a matter of fact, it has been of the greatest utility, stimulating investigation in order to test its accuracy or falsity, and thus indirectly causing to be added more knowledge to the sum of human learning. And in this lies the virtue of science, the investigation of the truth of every assertion, apart from, or if needs be in defiance of authority, by an appeal to fact.

Hyoid bone. The hyoid of the dog, like that of the frog, is derived from the hyoidean and part of the branchial arches.

It consists of a 'body,' transversely elongated, slightly curved, and continued at the two extremities into a larger anterior cornu or horn and a smaller posterior one. The anterior cornu consists of four distinct ossifications, of which the most dorsal one (tympano-hyal) is a small cylindrical bone, which becomes ankylosed to the hinder wall of the tympanic cavity; the others are much larger, and are named stylo-hyal, epi-hyal, and cerato-hyal.

Teeth. It has already been stated that the teeth of the dogfish and frog are of one kind only in either animal, and that the dentition is, therefore, said to be of the homodont type. In the dog we can distinguish three kinds of teeth, i.e. the **incisors** (Figs. 19 & 20, IN), **canines** (C), and **cheek-teeth** (PM & M), of which the latter are composed of **premolars**, or cheek-teeth which have milk predecessors, and **molars**, or those which have no predecessors. Since the dog possesses more than one form of tooth its dentition is said to be

heterodont; and since it has two sets of teeth, a **milk** or **deciduous** and a **successional** or **permanent**, it is also said to be **diphyodont**, in distinction to those mammals which have but one set, or are **monophyodont**, and those which have, in addition, a pre-milk dentition, with or without a trace of even a fourth set, or are **polyphyodont**.

In the dog's skull there are in the upper jaw, on either side, three incisors (Figs. 19 & 20, IN) lodged in the premaxilla, one canine (C) at the anterior extremity of the maxilla, four premolars (PRE.M), and two molars (not lettered in the figure), all lodged in the maxilla behind the canine. In the lower jaw there are three incisors, one canine, four premolars, and three molars.

A formula which indicates at a glance the number of teeth present is called the **dental formula**; for the dog, it may be constructed as follows, it being understood that the teeth of one side of the skull only are represented:—

$$\text{I}\,\frac{3}{3}\quad \text{C}\,\frac{1}{1}\quad \text{P.M}\,\frac{4}{4}\quad \text{M}\,\frac{2}{3}.$$

Or more briefly:

$$\frac{3.1.4.2}{3.1.4.3} = \frac{10}{11} = 21.$$

The full number of teeth is double that indicated in such a formula, i.e. 42.

The cranial foramina. The cranium is pierced by certain apertures for the transmission of the cranial nerves, and, as they are definitely and similarly related in all mammals, their position serves to indicate the limits of the segments of the skull.

The **optic foramen** (Fig. 19, OP.FOR) is situated at the posterior border of the orbito-sphenoid, and therefore lies in the frontal segment; it transmits the 2nd cranial (optic) nerve [1].

The **foramen lacerum anterius** (Fig. 19, FOR.ANT), **foramen rotundum** (FOR.ROT), and **foramen ovalis** (FOR.OV) all pierce the alisphenoid bone (AL) and belong to the parietal segment; of these, the first foramen transmits the first division, the second, the second division, and the third, the third division, of the 5th nerve, respectively; in addition, the first foramen also transmits the 3rd, 4th, and 6th cranial nerves.

The **foramen medium basis cranii** (Fig. 20, FOR.MED) is situated in the base of the skull, and lies between the basi-sphenoid and basi-

[1] For the cranial nerves, see chapter on 'Nervous System.'

occipital bones, and therefore between the parietal and occipital segments; it conveys the internal carotid artery.

The stylo-mastoid foramen lies just behind the external auditory meatus (Fig. 19, E.A.M), and the aperture of the **internal auditory meatus** just in front of it; of these two foramina, the meatus auditorius internus alone pierces the periotic bone; the stylo-mastoid foramen is only the aperture of a canal formed by the approximation of the tympanic bulla and periotic bone. The 7th and 8th nerves pass through the foramen in this latter bone; the 8th passes at once to the internal ear, while the 7th divides into two, the main branch of which passes along the stylo-mastoid canal, and the palatine branch through the internal meatus canal. The meatus auditorius internus thus lies between the parietal and occipital segments of the skull.

The **foramen lacerum posterius** (Fig. 20) is a wide slit-like aperture between the periotic bone (PER) and the exoccipital; it is, in fact, a notch in the latero-basal portion of the anterior margin of the occipital segment, and to this it belongs. It transmits the 9th, 10th, and 11th cranial nerves.

The **condylar foramen** lies immediately behind the foramen lacerum posterius, and pierces the exoccipital bone some way in front of the occipital condyle; it is a small foramen, and transmits the 12th cranial nerve.

The following foramina have no relation to the segments of the skull, and are not, therefore, of such importance: the **infra-orbital foramen** (Fig. 19, IN-OR.FOR) pierces the maxilla and communicates with the orbit of the eye; blood-vessels and the maxillary (2nd) division of the 5th nerve pass out through it from the orbit. The **lachrymal duct** (Fig. 19) pierces the lachrymal bone (LA), and places the orbit in communication with the nasal canal. The **naso-palatine** apertures (Fig. 20) lie just behind the incisor teeth; by means of them the buccal cavity and nasal canal would communicate, but that in life they are covered by membrane.

CHAPTER IV

THE VASCULAR SYSTEM, OR ORGANS OF CIRCULATION

THE vascular system consists of a hollow muscular organ, the **heart**, capable of rhythmically propelling the blood through a series of closed

tubes, the **blood-vessels**. Three kinds of the latter may be distinguished, according to their relation to the heart; those which carry blood from the central organ outwards to the tissues are called **arteries**, while those which carry it back again are known as **veins**. The arteries, by continually branching and forming smaller vessels or **arterioles**, and these branching to form still smaller vessels, ultimately give rise to a network of microscopic tubes called **capillaries**, the walls of which are composed of an exceedingly thin membrane. After ramifying in the tissues, these unite to form small veins, which in their turn form larger ones, and all of which ultimately pour their blood into the main veins going to the heart. The blood is thus running outwards in the arteries in the direction in which they branch, i.e. it travels from the larger to the smaller arteries, while in the veins it is travelling in the reverse direction, from the smaller to the larger ones; we therefore conveniently speak of the ramifications of arteries as **branches**, and those of veins as **factors**. Thus, a large artery breaks up into branches, but a large vein is formed by the union of its factors. With the division of an artery into branches, though the individual branches are smaller than the trunk one, their total cubical capacity is greater; and the same is true of the factors of veins. Hence the blood in passing through the arteries is travelling along an ever-widening channel, which attains its maximum width in the capillaries; in the veins, on the other hand, it is travelling through a channel that becomes narrower as it approaches the central organ or heart. Just as the velocity of a river varies with the width of its bed, so does the blood-stream with that of the channel through which it moves; as the channel widens, the current moves slower, and increases as the channel narrows. The blood therefore moves with greatest velocity in the main artery, with least velocity in the capillaries, and with a gradually increasing one as it passes through the veins towards the heart. Other physical factors besides width or narrowness of the channel determine the velocity, for the friction of the blood-stream against the walls of its vessels causes a retardation; and this friction is greatest in the capillaries. By means of a nervous mechanism the calibre of the arteries may be increased or diminished, so that in localized areæ of the vascular system the velocity of the blood-stream may be retarded or hastened.

In some cases the arterioles do not pass into capillaries, but open into irregular spaces among the constituents of the tissues; these are

usually lined by an epithelium which is, however, freely perforated, and in some cases does not exist at all. These spaces are known as **blood sinuses**, and most of the venous channels of the dogfish and of Invertebrata are of this nature, while those of the spleen of the frog and rabbit differ from them only in that they are sponge-like. The sinuses converge towards more definite channels and ultimately pass into veins.

In addition to the blood-vessels, another system of channels, containing a colourless fluid, and known as the **lymph system**, exists. It arises from the lacunæ which are situated among the constituents of nearly all tissues, and which by their confluence into larger channels, that gradually become lined by a definite epithelium, ultimately give rise to well-defined vessels, the **lymph-vessels**. These in their turn converge towards a few main trunks which empty their contents into one of the main veins of the body, very near its entrance to the heart. The function of the lymphatic system is to receive the liquid portion of the blood which has passed by transudation through the thin walls of the capillaries; this bathes and nourishes the tissues, and takes from them some of the waste products of their metabolism.

The blood consists of a liquid, the **plasma**, containing in suspension certain solid bodies, the **corpuscles**. The latter are of two kinds, **red** and **white**, of which the former are much more numerous than the latter. The white corpuscles are minute specks of protoplasm containing a nucleus; when examined under favourable conditions, viz. in a suitably saline solution, and at the temperature of the blood of the animal from which they were taken, each is seen to continually but slowly alter its form, in the same way that an amœba does, by throwing out blunt processes, in virtue of which it can move from one place to another and ingest solid particles.

The red corpuscles are those which give to blood its red colour, but they are red only when seen in mass, for examined singly or in a single layer under the microscope they are of a pale straw-colour. The colour is due to an iron-containing proteid, called **hæmoglobin**, one of the most important characters of which is its power of forming a loose and unstable chemical compound with oxygen or carbon dioxide, thus enabling it to carry the former to the tissues and the latter away from them. Blood in which the hæmoglobin is oxidized (oxy-hæmoglobin) is bright scarlet in colour and is called **arterial blood**, because as a rule, in the living body, it is contained in arteries; while blood in which the hæmoglobin has lost some of its oxygen and

taken up carbon dioxide (reduced hæmoglobin) is dark purple in colour and is known as **venous blood**, since it is found principally in veins or venous channels. The form and size of the red corpuscles differ in different animals. In the rabbit they are round, biconcave discs, devoid of a nucleus, and measure about $\frac{1}{3000}$ inch in diameter; in the frog and dogfish they are much larger, and are oval, biconvex, and nucleated. In the frog they measure about $\frac{1}{1000}$ inch in their long axis, and in the dogfish about $\frac{1}{1100}$ inch. In the rabbit they are nucleated in early embryonic life, but at birth, as in all mammals, all the red corpuscles are non-nucleated. The red corpuscles are composed of a colourless, structureless, and transparent framework, or **stroma**, infiltrated in all parts by the red colouring matter, hæmoglobin. The stroma is elastic, so that the corpuscles can adapt themselves to the form of the vessels through which they move. The plasma consists of about 90% of water, with about 8% of proteids, i.e. paraglobulin, serum-albumin, and fibrinogen, in solution; the remaining 2% consists of the chlorides, sulphates, and phosphates of sodium and potassium, with other salts and a little fat.

The lymph is a fluid contained in the lymph-vessels, and is very similar in nature and composition to the plasma of the blood, from which, indeed, it is derived. It contains suspended in it **lymph corpuscles**, bodies that are identical in all respects with the white corpuscles (**leucocytes**) of the blood.

The Heart.

Dogfish. The heart of the dogfish (Fig. 22) is composed of three chambers, of which two are thin-walled and the other thick and very muscular. It lies in a triangular chamber that is situated dorsally to the coracoid cartilage, and the apex of which is directed forward (Fig. 25, PER). This chamber is the **pericardial chamber** or **pericardium**, and the study of its development shows that it is the anterior portion of the cœlom constricted off almost completely from the main portion, with which it still retains some connexion by a single, median, tubular canal, the **pericardio-peritoneal canal**; this latter is lined with a definite membrane, continuous with the peritoneum of the cœlom.

Of the three chambers of the heart, the posterior (Fig. 22, A & B, SIN. VE) is thin-walled and elongated laterally into two horns, which are continuous with the Cuvierian veins or ducts of either side that

return to the heart blood brought to them by veins from all parts of the body; this chamber is the **sinus venosus**, and it opens (Fig. 22, B) by a median slit-like aperture, guarded by two membranous pocket-like folds, or valves, into the next and much larger chamber (ATR), the **atrium**. The atrium is thin-walled, and the valves which guard the opening between it and the sinus venosus are disposed in such a way that they readily allow the blood to pass from the latter to the former, but not in the reverse direction. The atrium in turn opens

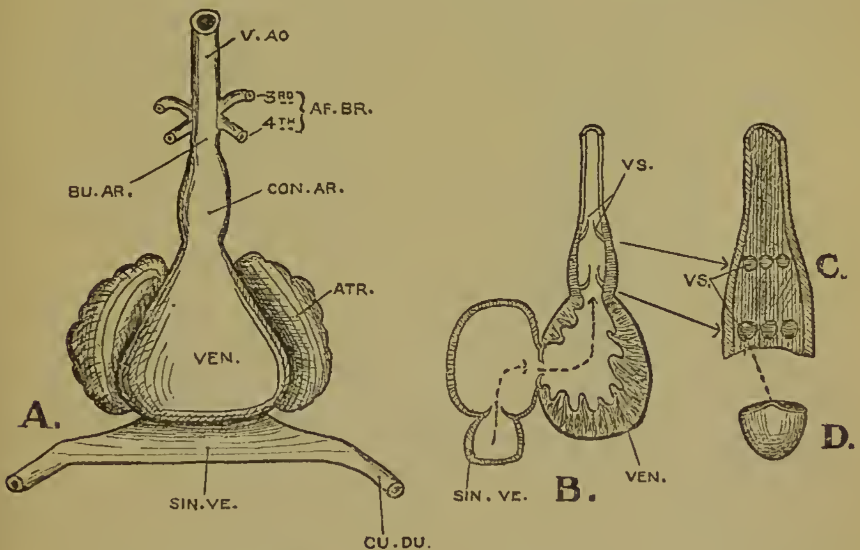

FIG. 22. The heart of the Dogfish (*Scyllium*). A. Ventral view. B. Median vertical section of heart, showing the chambers. C. The conus and bulbus arteriosus cut open and reflected to show the semilunar valves within. D. A single semilunar valve enlarged four times. AF.BR = third and fourth afferent branchial arteries; ATR = atrium; BU.AR = bulbus arteriosus; CON.AR = conus arteriosus; CU.DU = Cuvierian duct or vein; SIN.VE = sinus venosus; VEN = ventricle; VS = semilunar valves; V.AO = ventral aorta.

into the very thick-walled **ventricle** (VEN) by a single slit-like, transversely arranged aperture guarded by two valves, which prevent the return of the blood back to the atrium. The ventricle is somewhat globular in form, its walls are muscular and spongy, and anteriorly it is produced into a cylindrical organ (CON.AR), the tubular cavity of which is continuous with that of the ventricle. This tubular continuation of the ventricle is called the **conus arteriosus**, and, like it, is contractile; it contains upon its inner surface two sets of semilunar or pocket-like valves (VS) arranged in two rows (Fig. 22, C, VS), one just in front of the ventricle, viz. at the base of the conus, and the

other at about the middle of the length of that; both sets consist of three valves, each of which is thin and membranous at its edges, but thick in its central part.

The conus arteriosus is continued forward in the median line as the **ventral aorta** (Fig. 25, VE.AO), the basal portion of whieh, viz. that which is the immediate continuation of the eonus, is called the **bulbus arteriosus** (Fig. 22, A, BU.AR), and does not, like the former, contract with the ventricle.

An inspection of Fig. 22, B, will reveal the fact that the three chambers of the heart are arranged along a loop in the form of the letter S; this will be rendered more manifest if the figure is turned round to the right through a right angle. The sinus venosus is then situated on the top loop, the atrium on the middle one, and the ventricle on the bottom loop. The relative arrangement of the parts on an S-shaped loop is a primitive condition, and is one through which the heart of all Vertebrates, *Amphioxus* excepted but man included, passes in the course of its development.

Frog. The heart of the frog, though somewhat primitive in virtue of a well-developed sinus venosus, yet exhibits a considerable advance upon that of the dogfish, in that the atrium is divided into **right and left auricles** (Fig. 23, C, R.AUR, L.AUR) by a **septum atriorum.** This is an advance that is correlated with the development of lungs, since in all lung-breathing animals both the aërated blood from these organs and that from the body in general is returned to the heart, and it is necessary for the proper distribution of the two streams that they should be kept apart while travelling through the atrium. The two auricles, of which the right is larger than the left, do not lie dorsally to the ventricle as in the dogfish, but become carried forward during their development and lie anteriorly to it. The right auricle receives the venous blood from the sinus venosus (Fig. 23, B, O.SIN.VE and C), while the left receives it from the pulmonary veins (Fig. 23, B, PUL.VE), which return it from the lungs. The **ventricle** (VEN) is conical, and the spongy meshwork of whieh its wall is largely composed partially invades and almost obliterates its single cavity; as the result of this, the two streams of blood which enter it, i. e. the impure from the right and the pure (aërated or oxygenated) from the left auriele, do not completely mix before they are propelled from it by its contraetion. The two auricles open into the single ventricle by a slit-like opening, the **atrio-ventricular aperture**, which is guarded by two poeket-like **atrio-ventricular valves** (AUR-VEN.V) that are so disposed

that the blood is prevented from returning to the auricles upon the contraction of the ventricle. The sinus venosus (Fig. 23, B, SIN.VE) is a thin-walled, triangular sac situated upon the dorsal surface of the heart, and opening into the left-hand side of the right auricle (O.SIN.VE); its apex is directed backwards and receives the blood from the **post-caval** (inferior vena cava) **vein** (PC.); the two angles of the base are

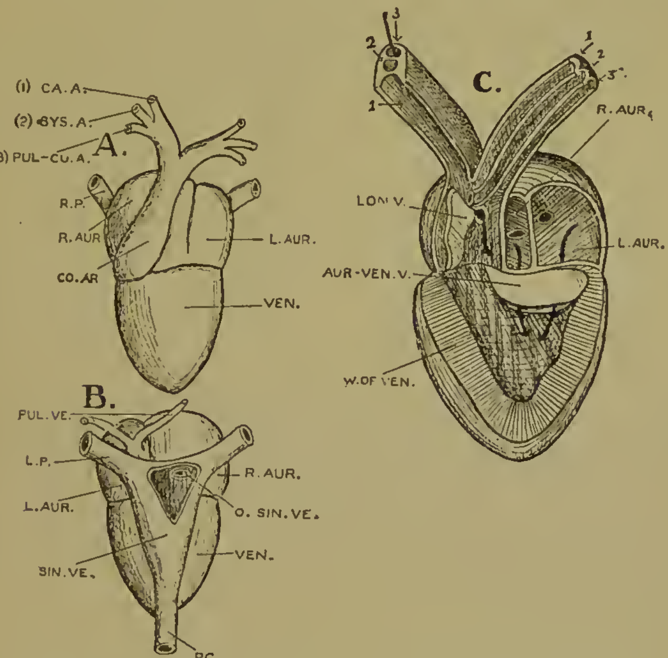

FIG. 23. A. Ventral view of heart of Frog (*Rana*). B. Dorsal view of same. C. A ventral dissection to show interior of cardiac chambers. AUR-VEN.V = atrio-ventricular valves; CA.A = carotid arch; CO.AR = conus arteriosus (basal portion of truncus arteriosus); L.AUR = left auricle; LON.V = longitudinal valve; L.P = left precaval vein; O.SIN.VE = communication of sinus venosus with right auricle; PC = post-caval vein; PUL.VE = pulmonary veins; PUL-CU.A = pulmo-cutaneous arch; R.AUR = right auricle; R.P = right precaval vein; SIN.VE = sinus venosus; SYS.A = systemic arch; VEN = ventricle; W. OF VEN = wall of ventricle; 1, 2, 3 = first, second, and third arterial arches respectively. The semilunar valves at the top and bottom of synangium are not represented, for the sake of clearness. Two arrows are placed in the atrio-ventricular aperture leading from the auricles to the ventricles, and another one in the third arch of the right side.

respectively continued into the very short left and right **precaval** (superior venæ cavæ) **veins** (L.P. & R.P).

From the right-hand lateral corner of the ventricle there arises a tubular organ, the **truncus arteriosus**, which is the basal portion of the arteries that arise from it. It consists of two parts, a proximal (situated nearer the ventricle) and a distal, marked off internally from

each other by three semilunar (pocket-like) valves. The proximal portion (Fig. 23, CO.AR) is called the **pylangium**, and corresponds to the conus arteriosus of the dogfish; it contains a valve (LON.V) longitudinally arranged, the attached border of which runs a somewhat spiral course; the valve is so disposed that it can be moved from the ventral to the dorsal surface of the interior of the pylangium, so that it can lie alternately upon either surface. The opening of the pylangium into the ventricle is guarded by three semilunar valves, and there are three similar valves at its junction with the **synangium** or distal portion of the truncus arteriosus. The synangium—which corresponds to the bulbus arteriosus of the dogfish—divides very quickly into right and left trunks, each of which gives rise to three arterial arches, named from before to behind, the **carotid** (1), **systemic** (2), and **pulmo-cutaneous** (3) **arches** respectively (Fig. 23, A and C). Of these arches the internal openings of the second and third are larger than those of the first, and those of the third are, moreover, covered by the anterior extremity of the spiral valve when that lies upon the dorsal wall of the pylangium (Fig. 23, C).

The heart is enclosed within a double-layered membranous sac, the **pericardium**, of which the inner layer, i. e. that closely investing the heart itself, is called the **visceral**, and the outer the **parietal layer**. Between the two layers is a potential space called the pericardial cavity, which is filled with lymph, and represents a portion of the cœlom that has become completely cut off from the remainder during the course of development; up to the period of the metamorphosis (change from tadpole to frog), however, there is free communication between the pericardial cavity and that of the cœlom by two apertures in the dorso-posterior region of the pericardium.

Flow of blood through the heart. The passage of the blood through the frog's heart is apparently somewhat complicated, owing to the mechanism of the truncus arteriosus. The blood is returned from all parts of the body to the sinus venosus, whence it passes at once to the right auricle; from the lungs it is returned to the left auricle by the pulmonary veins. From the two auricles it is pumped into the ventricle by their simultaneous contraction, and within this the two blood-streams do not readily mix, owing to the ventricular cavity being largely filled by the reticular meshwork of which the wall is almost entirely composed. It follows that the right side of the ventricle contains the impure blood poured into it by the right auricle, and the left the pure and oxygenated blood driven in by the left auricle,

while in the middle, at the plane of junction between the two kinds, there will be mixed blood. Upon the contraction of the ventricle the first portion of blood to leave it will be that nearest the aperture of the truncus arteriosus upon the right side; and this is wholly venous blood, which as it passes into the truncus, does so at first dorsally to the spiral valve, since at the commencement of the ventricular contraction this lies against the ventral wall; but some portion of the blood—the amount of which progressively increases—getting between the valve and the wall, ultimately carries the valve over to the dorsal wall of the truncus and occludes the apertures of the pulmo-cutaneous arteries. The first portion of blood thus thrown into the truncus arteriosus passes into the artery just mentioned, since the apertures of this are the first which it meets in its course; but by the time that the wholly venous blood of the right side of the heart has passed into the pulmonary circulation, the longitudinal spiral valve, as above described, has closed the apertures of the third arch (pulmo-cutaneous), so that the next portion of blood, i. e. mixed, to pass along the truncus is prevented from entering, and has two routes open to it, for it may either pass into the systemic or the carotid arch. The apertures of the latter arch, however, are much smaller than those of the former, and moreover the resistance offered by the passage of fluid through the carotid is much greater than that in the systemic, both on account of its smaller calibre and also because that calibre, already small, is still further reduced by the intrusion into it of the carotid gland (Fig. 28, CAR.G); and since fluid will flow in the path of least resistance, the second portion of blood, which is mixed venous and arterial, flows into the second or systemic arch. It flows into it, however, quicker than it can be carried away by the peripheral system of arteries and capillaries into which it leads, in consequence of which its elastic walls become distended, and press with increasingly greater force upon the blood within it, in consequence of which the resistance ultimately becomes greater in the systemic than in the carotid arteries. The third and last portion of blood, i. e. the wholly arterial blood of the left side of the heart, when it arrives at the synangium, therefore finds it easier to pass through the carotid arch than through the systemic.

It follows, therefore, from this distribution of the blood, that the lungs are supplied with wholly venous blood, the viscera and body in general with mixed blood, and the brain and spinal cord by arterial blood; a distribution which in some measure explains the sluggish

habits of the frog, since the motor tissues of the body are not supplied with unalloyed arterial blood (Plate I, Fig. 2).

Rabbit. The heart of the rabbit is among the most highly organized types, and is essentially the same as that of man. It differs from that of the dogfish and frog inasmuch as the sinus venosus is absent, it having become incorporated with the wall of the right auricle and the base of the caval veins; and in the course of development the ventricle as well as the atrium is perfectly divided into two chambers (Fig. 24, L.VEN & R.VEN) by an **inter-ventricular septum**, so that the arterial and venous blood are kept continually apart.

The two auricles (Fig. 24) lie anteriorly to the two ventricles; each is produced ventrally into a tongue-shaped portion, the **auricular appendix** (Fig. 24, B, L.AUR.AP. & R.AUR.AP), the wall of which is thicker than that of the auricle in general, and is supported internally by a meshwork of muscular bands, the **musculi pectinati**. The **septum auricularum** [1] is characterized by an oval area thinner than the rest of the wall, the **fossa ovalis**; this marks the position where an opening, secondarily acquired, existed in the embryo before the lungs became functionally active, and that allowed the blood to pass direct from the right auricle into that of the left, thence into the left ventricle, and so to the systemic circulation, without first going to the right ventricle as in extra-embryonic life.

The systemic veins, i. e. the **right** and **left precavals** (Fig. 24, L.P, R.P) (R. & L. **anterior venæ cavæ**), and the **post-caval** (P.C) (**posterior vena cava**), open into the right auricle by separate apertures, that of the latter vein being partially guarded by a membranous fold, the **Eustachian valve**, which lies between the apertures of the post-caval and the left precaval. The valve represents the **right venous valve** of the early embryonic heart, and which in conjunction with a similar left valve guarded the orifice of the sinus venosus into the right side of the right auricle. In later embryonic life, when the sinus venosus becomes incorporated with the right auricle and the base of the great veins, the left valve disappears, and the right persists in a modified form throughout life as the **Eustachian valve**; up to the period just preceding birth it plays the important function of directing the blood from the post-caval through the foramen ovale into the left auricle, and thus prevents the blood from passing into the right ventricle; such an act would be quite useless, since the lungs, to which the blood from the right ventricle would pass, are

[1] Septum atriorum of the frog's heart.

incapable of oxygenating the blood flowing through them during embryonic (intra-uterine) life.

The left auricle receives the four **pulmonary veins** (Fig. 24, A, R.PUL.V ; *the two left ones are not lettered*), two from either lung, which enter its dorsal wall in the U-shaped cavity formed by the two precavals ; they return oxygenated (arterial) blood to the heart.

The aperture between the right auricle and the corresponding ventricle, called the **auriculo-ventricular aperture**, is wide and crescentic in form, and is guarded by three triangular membranous flaps, together forming the **tricuspid valve**; the flaps are attached

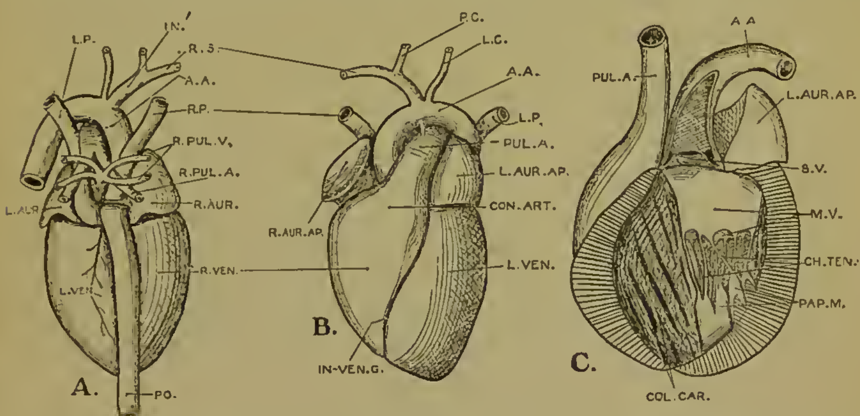

FIG. 24. Heart of Rabbit (*Lepus*). A. Dorsal view. B. Ventral view. C. The left ventricle and base of aorta cut open to show the mitral valve, papillary muscles, and semilunar valves. A.A = aortic arch; CON.ART = conus arteriosus; COL.CAR = columnæ carneæ; CH.TEN = chordæ tendinæ; IN-VEN.G = inter-ventricular groove; IN′ = innominate artery; L.AUR = left auricle; L.AUR.AP = left auricular appendage; L.P = left precaval; L.C = left common carotid; L.VEN = left ventricle; M.V = mitral valve; PC = post-caval; PUL.A = pulmonary artery; PAP.M = musculi papillares; R.P = right precaval; R.PUL.V = right pulmonary veins; R.PUL A = right pulmonary artery; R.AUR = right auricle; R.AUR.AP = right auricular appendage; R.S = right subclavian artery; R.VEN = right ventricle; S.V = semilunar valves. The ductus Botalli is not lettered, but is represented in B as a small string connecting the arch of the aorta with that of the pulmonary artery.

round the margin of the aperture, and their free borders are connected by tendinous cords, called **chordæ tendineæ** (CH.TEN), to muscular processes of the ventricular wall, called **musculi papillares** (PAP.M), the object of which is to prevent the valves being forced back into the auricular cavity upon the contraction of the ventricle. The left auriculo-ventricular aperture is circular in form, and is guarded by a membranous **mitral valve** (Fig. 24, C, M.V), consisting of two flaps, connected by their free borders to the wall of the ventricle in a similar manner to that of the right, but the musculi papillares are much larger.

In correlation with the greater work which it has to perform, the wall of the left ventricle is very much thicker than that of the right, and the **columnæ carneæ** (COL.CAR) (muscular columns on the internal surface of the ventricular wall) and musculi papillares are more strongly developed.

The left anterior ventral corner of the right ventricle is a little prolonged, and at the summit of this the **pulmonary artery** arises; the prolongation (CON.ART) is the last trace of the embryonic conus arteriosus. The orifice of the pulmonary artery is guarded by three semilunar valves (C, S.V), so disposed that blood can flow freely from the ventricle to the artery, but not vice versa, and their efficiency is increased by slight dilatations of the arterial wall, called **sinuses of Valsalva**, immediately beyond the attachment of the valves.

The **aorta** (Fig. 24, B & C, A.A) arises from the right-hand. antero-ventral angle of the left ventricle, and its orifice is guarded (C, S V) in precisely the same manner as that of the pulmonary artery.

The wall of the heart itself is supplied with blood by two **coronary arteries** which arise from two of the sinuses of Valsalva in the aorta, and return the blood to the right auricle by a **coronary vein** that enters the left precaval just before that enters the auricle.

The heart is enclosed in a double-layered sac, the **pericardium**, of a similar nature to that of the frog.

Flow of blood through the heart. The venous blood from all parts of the body is poured into the right auricle by the caval veins, thence by the contraction of the auricular walls it is propelled into the right ventricle, where some of it getting between the tricuspid valve and the ventricular wall, the valvular flaps are gradually raised until the auriculo-ventricular aperture is partly closed. Upon the ventricle suddenly contracting, the blood is driven against the valve, and forcing the flaps against each other, completely closes the auriculo-ventricular aperture, so that but one course is left for it to pursue, i.e. through the orifice of the pulmonary artery to the lungs. It is carried from the capillaries of the lungs, where it is oxygenated, to the left auricle of the heart by the four pulmonary veins, whence it passes to the left ventricle, and by its sudden contraction is driven into the aorta and its branches. From these it passes through the capillaries of the body and alimentary canal, thence converges through numerous venous channels to the caval veins, and thus back to the right auricle.

It will thus be seen that the right side of the heart contains venous blood brought back from all parts of the body, and which is sent to

the lungs to be oxygenated (arterialized); that the left side contains arterial blood, which is returned direct from the lungs, and is sent through the aorta all over the body.

During life the arteries are always full, so that at each contraction of the ventricle the blood is driven into them against considerable resistance, arising from the friction between the moving stream and the minute capillaries, through which the blood cannot pass as rapidly as that thrown into the arteries at each contraction. In order to accommodate the blood thus propelled into arteries already full, the arterial walls distend and thus widen the calibre of the arteries; but their elastic recoil coming into play, the blood is subjected to a pressure which tends to drive it both backwards and forwards, and it is obvious that were there not some provision to prevent it the blood would flow back again into the ventricles. This is prevented by the three semilunar valves which are situated at the root of the aorta and pulmonary artery, and which, as soon as the blood begins to flow backwards, are forced back so that they meet each other along their free edges and completely close the orifice. The pressure of the elastic arterial walls upon the blood-stream is continuous, and since fluids are incompressible, results in it being driven forward under pressure; this pressure is known as the **blood pressure**.

The Arterial System.

Dogfish. The **ventral aorta** (Fig. 25, VE.AO) arises from the conus arteriosus by a slightly dilated portion, the **bulbus arteriosus** (Fig. 22), and is continued forward in the middle line between the gills. At its anterior termination it divides into two branches, one of which turns outwards to the left, and the other to the right; both again divide into an anterior and posterior branch, of which the former, called the first **afferent branchial artery** (1, AF.BR.A), runs along the outer border of the hyoid arch (HY.A) and supplies the anterior half of the first gill-sac[1]; the latter branch, called the second **afferent branchial artery** (2, AF.BR.A), runs along the outer border of the first branchial arch (Fig. 17, CER.BR) and supplies the posterior hemibranch of the first gill-sac[1], and the anterior hemibranch of the second. Farther back along the ventral aorta (Fig. 25) there arises from either side three other arteries, known respectively as the third, fourth, and fifth **afferent branchial arteries** (3, 4, 5, AF.BR.A), and

[1] For definition of gill-sac and hemibranch, see p. 172.

which, running along the outer borders of the second, third, and fourth branchial arches (Fig. 17) respectively, each supplies the posterior and anterior hemibranchs of the two adjacent gill-sacs. The fifth

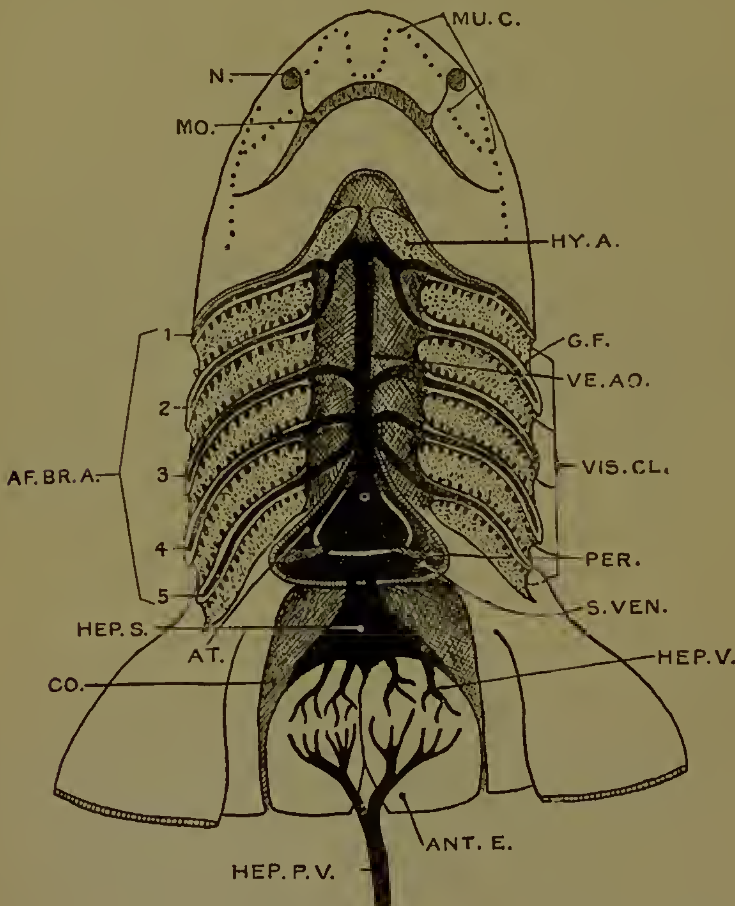

FIG. 25. Ventral dissection of Dogfish, showing ventral aorta and afferent branchial arteries, pericardium and heart; and the hepatic region of the hepatic-portal system somewhat semi-diagrammatically represented. The skin and ventral muscles have been removed, the gill-sacs cut open and dissected down to the level of afferent arteries. AF.BR.A. = afferent branchial arteries; ANT.E = anterior end of liver; AT = atrium; CO = cœlom or body cavity; G.F. = gill filaments; HEP.P.V = hepatic-portal vein; HEP.S = hepatic sinus; HEP.V = hepatic veins; HY.A = hyoid arch; MO = mouth; MU.C = mucous canals; N = nostril; PER = pericardium; S.VEN = sinus venosus; VE.AO = ventral aorta; VIS.CL = gill or visceral clefts.

branchial arch bears no gill, and is, therefore, not supplied by a branchial artery; and as the hyoid arch only bears a posterior hemibranch, the five branchial arteries only supply four holobranchs and a hemibranch.

The blood carried to the gills by the afferent branchial arteries is taken away from them by the four **epibranchial arteries** (Fig. 26, EP.A). Each epibranchial artery is formed by the union of two **efferent branchial arteries** (EF.A), one of which receives the blood from the posterior and the other from the anterior hemibranch of each gill-sac; the efferent branchial arteries form loops and are continuous round the inner ventral limits of the gill-clefts, and in addition the anterior limb of each loop is connected with the posterior limb of the loop next in front by a short horizontal vessel. The posterior hemibranch of the last gill returns its blood into a half loop (seen just behind E.B in Fig. 26) which is connected by a horizontal vessel with the posterior limb of the fourth epibranchial artery (4th EP.A). The anterior limb (first efferent branchial) of the first loop gives origin to two other arteries, i.e. the **common carotid artery** (Fig. 26, C.C) and the **hyoidean artery**; the former arises from it near the point where it joins the epibranchial artery, and the latter from about the middle of its length in line with the connecting horizontal vessels. If the student bears in mind the fact that the efferent branchial loops arise from that portion of the gills which lie in the floor of the pharynx and follow them round to the roof, where the efferent arteries join the epibranchials, he will understand why, in the figure where the floor of the pharynx has been cut away, the hyoidean artery does not appear. The artery arises from the first efferent branchial as it is bending round towards the roof in the side wall of the pharynx, and this part is just without the limits of the efferent arteries represented in the figure. The common carotid divides into two branches, the internal of which, called the **internal carotid artery** (Fig. 26, IN.C), supplies the brain, and the external, the **external carotid artery** (EX.C), passing across the floor of the orbit of the eye, supplies the upper jaw and snout. The hyoidean artery supplies the pseudobranch or spiracle[1], thence passing forwards and inwards, and penetrating the skull-case, forms an anastomosis with the internal carotid artery of the other side, from which arise many branches that supply the brain.

The **dorsal aorta** (Fig. 26, D.A) is the main artery of the body; it takes its origin from the four epibranchial arteries and in part from the common carotid artery, and runs as a median vessel along the whole length of the body, immediately ventrad of the vertebral column. The posterior portion, which traverses the region of the

[1] See chapter on 'Organs of Respiration.'

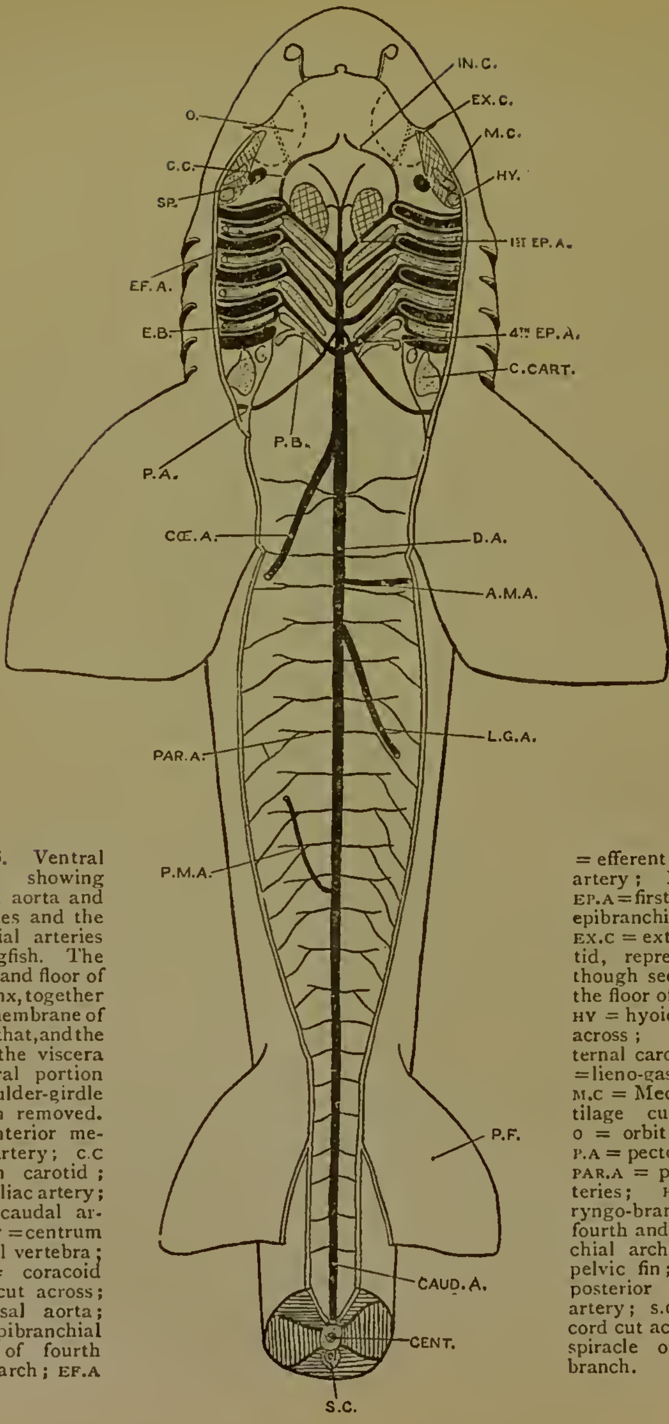

FIG. 26. Ventral dissection showing the dorsal aorta and its branches and the epibranchial arteries of the Dogfish. The lower jaw and floor of the pharynx, together with the membrane of the roof of that, and the whole of the viscera and ventral portion of the shoulder-girdle have been removed. A.M.A = anterior mesenteric artery; C.C = common carotid; CŒ.A = cœliac artery; CAUD.A = caudal artery; CENT = centrum of a caudal vertebra; C.CART = coracoid cartilage cut across; D.A = dorsal aorta; E.B = epibranchial cartilage of fourth branchial arch; EF.A = efferent branchial artery; 1st & 4th EP.A = first and fourth epibranchial artery; EX.C = external carotid, represented as though seen through the floor of the orbit; HY = hyoid arch cut across; IN.C = internal carotid; L.G.A = lieno-gastric artery; M.C = Meckel's cartilage cut across; O = orbit of eye; P.A = pectoral artery; PAR.A = parietal arteries; P.B = pharyngo-branchials of fourth and fifth branchial arches; P.F = pelvic fin; P.M.A. = posterior mesenteric artery; S.C = spinal cord cut across; SP = spiracle or pseudo-branch.

tail, is called the **caudal artery** (CAUD.A), and runs in the hæmal arches of the caudal vertebræ (Fig. 1). The first branches that arise from it are those supplying the pectoral fins and called the **subclavian** or **pectoral arteries** (Fig. 26, P.A). The **cœliac artery** (CŒ.A), supplying the proximal portion of the stomach, the liver, the anterior part of the intestine and pancreas, arises from the aorta a very short way behind this. The greater portion of the intestine, the rectum, and the genital organs are supplied by the **anterior mesenteric artery** (A.M.A), which arises from the aorta a little way behind the cœliac artery. Immediately behind, the **lieno-gastric artery** (L.G.A) takes its origin, and passes to the loop of the stomach, the spleen, and to part of the pancreas. The **posterior mesenteric artery** (P.M.A) is an exceedingly small one, and arises from the aorta behind the last-named artery, and supplies the rectal gland. The body-wall is supplied by a series of segmentally arranged arteries, the **parietal arteries** (PAR.A), arising at intervals along the whole length of the aorta, and in the region of the kidneys giving off small **renal arteries** which supply those organs. The pelvic fins are supplied by a pair of **iliac arteries** which arise from the aorta in the posterior limits of the body cavity.

Frog. As already mentioned the principal arteries of the body arise as three arches on either side, from the truncus arteriosus (Fig. 128); they are named in order from before to behind, the **first** or **carotid** (C.CAR.A); the **second** or **systemic** (SYS.AR); and the **third** or **pulmo-cutaneous arch** (PUL-CUT.A).

Carotid Arch. In the tadpole this arch is represented by the first branchial artery which supplies the first gill-arch. A very short distance from its origin the arch bears, in the adult, a dilated portion, called the **carotid gland** (Fig. 27, CAR.G), the interior of which is spongy, and is composed of bands or trabeculæ of unstriped muscle. The facts of development show that it is the modified and elaborated direct passage between the afferent and efferent branchial vessel of the tadpole, and is not, as was formerly believed to be the case, a persistent and modified portion of a gill (Fig. 32, D.O). Immediately beyond the gland the arch gives off two branches, one of which, the **lingual artery** (LIN.A), supplies the hyoid, tongue, and thyroid gland; the other, the **common carotid artery** (C.CAR.A), turns round the œsophagus and runs forward to the base of the skull, where it gives off the following branches:—

1. The **internal carotid**, which supplies the brain.

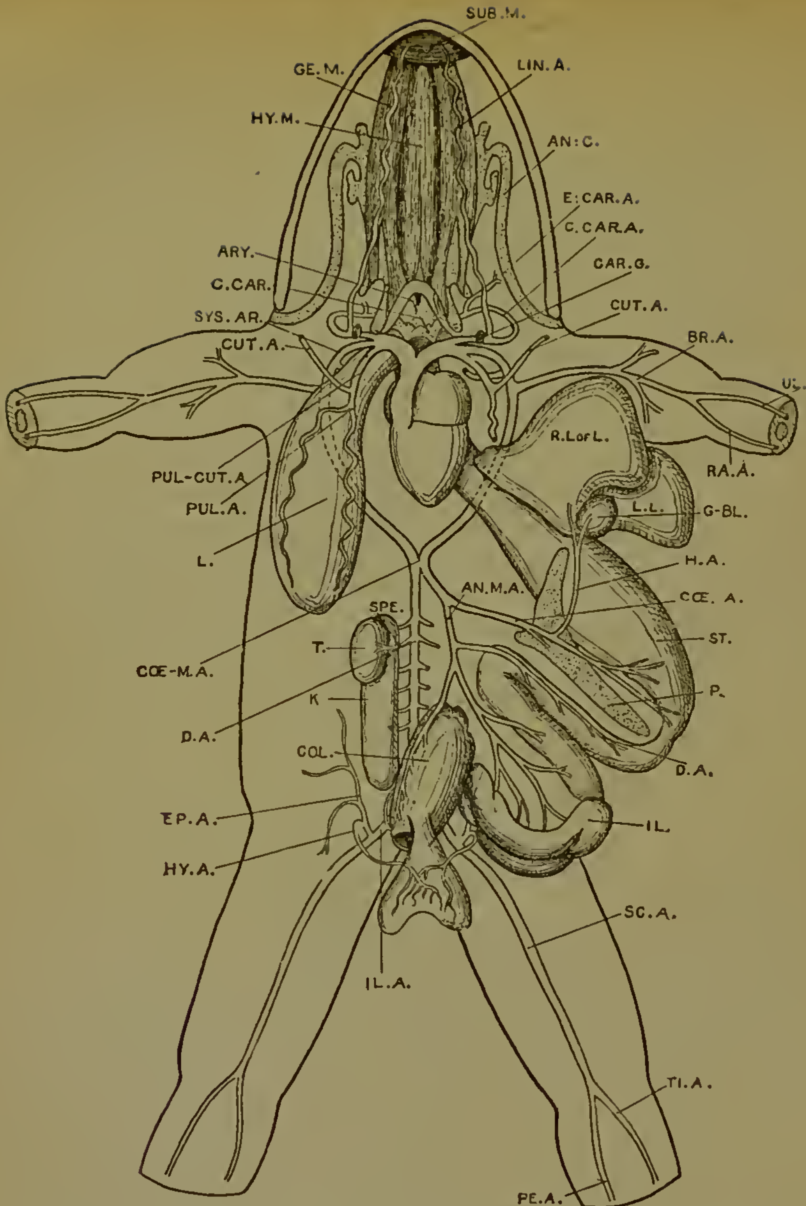

FIG. 27. Ventral dissection to show the principal arteries of Frog (*Rana*). The ventral body-wall and pectoral girdle have been removed and the viscera turned over to the left; the Wolffian (urinary) bladder has been turned backwards. AN.C = anterior cornua of hyoid plate; ARY = arytenoid cartilage of larynx; AN.M.A = anterior mesenteric artery; BR.A = brachial artery; C.CAR = cricoid cartilage of larynx; C.CAR.A = common carotid artery; CAR.G = carotid gland; CŒ.A = cœliac artery; CŒ-M.A = cœliaco-mesenteric artery; CUT.A = cutaneous artery; COL = colon or large intestine; D.A (to reader's left) = dorsal aorta; D.A (to right) = duodenal artery; E.CAR.A = external carotid artery; EP.A = epigastric artery; G-BL = gall-bladder; GE.M = genio-hyoideus muscle; HY.M = hypoglossus muscle; H.A = hepatic artery; HY.A = hypogastric artery; IL = ileum or small intestine; IL.A = iliac artery; K = kidney; L = lung; LIN.A = lingual artery; L.L = left lobe of liver; PUL.A = pulmonary artery; PUL-CUT.A = pulmo-cutaneous artery; P = pancreas; PE.A = peroneal artery; RA.A = radial artery; R.L of L = right lobe of liver; SC.A = sciatic artery; SPE = spermatic artery; SYS.AR = systemic arch; SUB.M = submentalis muscle; ST = stomach; T = testis; TI.A = tibial artery; UL.A = ulnar artery.

2. The **external carotid** (E.CAR.A), which divides into :—

(*a*) The **ophthalmic artery**, supplying the coats of the eye.

(*b*) The **anterior** and **posterior palatine arteries**, supplying the mucous membrane of the palate.

Systemic Arch. In the tadpole this is represented by the second branchial artery, which supplies the second branchial arch. In the adult frog it is the middle of the three arches (SYS.AR) ; the arch turns obliquely round the œsophagus in a wide curve on either side, and runs towards the vertebral column; at the level of about the sixth vertebra the two arches meet, and apparently unite to form the **dorsal aorta** (D.A, to the reader's left), which runs along the vertebral column to the posterior end of the cœlom. As a matter of fact, the dorsal aorta is the direct continuation of the right systemic arch, just as the cœliaco-mesenteric artery (CŒ-M.A) is the continuation of the left. But at the point where the two arches meet there is a communication between them. At the hinder end of the cœlom the dorsal aorta divides into the two **iliac arteries** (IL.A), which pass outwards to the thigh, and are continued in either leg as the **sciatic arteries** (SC.A) to the end of the femur, when each divides into **tibial** (TI.A) and **peroneal** (PE.A) **arteries** that run in the calf of the leg towards the foot. The **hypogastric** (HY.A) and **epigastric** (EP.A) **arteries** arise from the iliac artery, the former supplying the bladder and the latter some of the muscles of the hip-joint and those of the ventral abdominal wall.

Cœliaco-mesenteric artery (CŒ-M.A). This apparently arises from the dorsal aorta immediately after the junction of the two systemic arches, but is in reality the continuation of the left systemic arch ; it very quickly divides into two branches, the **cœliac artery** (CŒ.A), supplying the stomach, gall-bladder, and liver, and the **anterior mesenteric artery** (AN.M.A), supplying the spleen, pancreas, small intestine, duodenum, and anterior portion of the large intestine.

Posterior mesenteric artery (**hæmorrhoidal artery**). A very small artery arising from the posterior end of the dorsal aorta, and supplying the posterior portion of the large intestine.

Arteries given off from the Systemic Arch.

1. **Œsophageal arteries.**

2. **Occipito-vertebral artery.** The origin of this is seen on the left-hand side of Fig. 27, arising from the inner side of the systemic arch just in front of the origin of the brachial artery (BR.A). It divides into two, the posterior of which, **vertebral artery**, courses

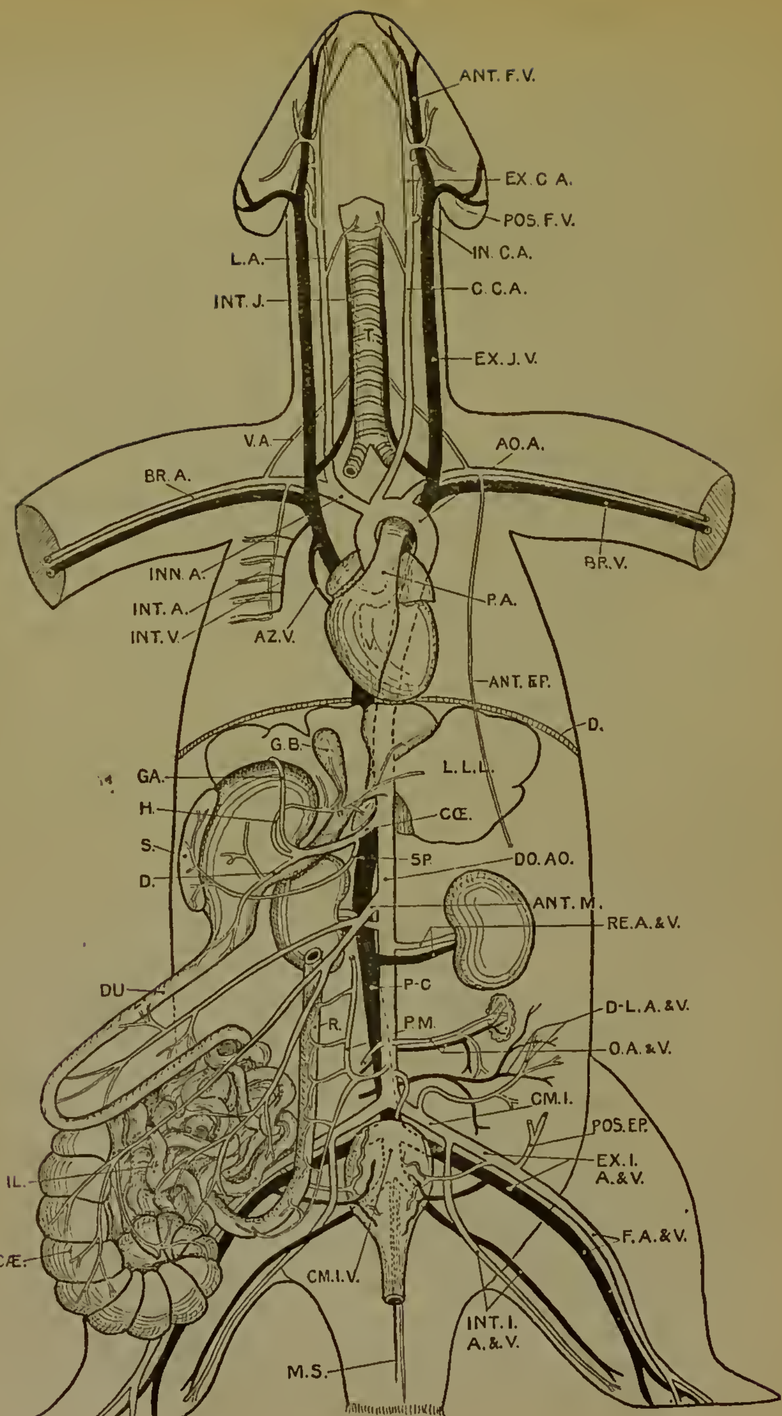
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FIG. 28.

backwards along the transverse processes of the vertebræ, and the anterior one, the **occipital artery**, runs forward and supplies the mucous membrane of the nose, the upper jaw, tympanic membrane, and skin of the head.

3. **Subclavian artery.** This arises from the arch immediately behind the occipito-vertebral artery, and runs outwards alongside of and ventrally to the brachial nerve, to reach the arm, where it is continued as the **brachial artery** (BR.A), which in the fore-arm divides into **ulnar** (UL.A) and **radial** (RA.A) **arteries.**

Pulmo-cutaneous arch (PUL-CUT.A). In the tadpole this is represented by the fourth branchial arterial arch, the third one completely disappearing. In the adult the **pulmo-cutaneous arch** divides soon after its origin into two, the posterior branch of which, the **pulmonary artery** (PUL.A), supplies the lung, while the anterior one, the **cutaneous artery** (CUT.A), passes to the skin and forms a rich anastomosis that extends to the posterior end of the trunk. The presence of such a complex anastomosis in the skin is indicative of a respiratory function, and during the hibernating period, when the animal is buried away, often beneath mud, respiration is doubtless wholly carried on by means of the blood circulating through it.

Description of Fig. 28.

Ventral dissection of the Rabbit (*Lepus*), to show main arterial and venous vessels. The arteries are represented in line and the veins in solid black. The ventral portion of the pelvic and pectoral girdles have been removed, as well as the body-wall and ribs. The viscera has been turned over to the animal's right. AO.A = aortic arch; ANT.F.V = anterior facial vein; ANT.EP = anterior epigastric; ANT.M = anterior mesenteric artery; AZ.V = azygos vein; BR.A = brachial artery; BR.V = brachial vein; C.C.A = common carotid artery; CŒ = cœliac artery; CÆ = cæcum; CM.I = common iliac artery; CM.I.V = common iliac vein; D (to reader's right) = diaphragm; D (to reader's left) = duodenal branch of cœliac artery; DO.AO = dorsal aorta; DU = duodenum; D-L.A & V = dorso-lumbar artery and vein; EX.C.A = external carotid artery; EX.J.V = external jugular vein; EX.I.A & V = external iliac artery and vein; F.A & V = femoral artery and vein; GA = gastric artery; G-B = gall-bladder; H = hepatic artery; IN.C.A = internal carotid artery; INT.I.A & V = internal iliac artery and vein; IL = ileum or small intestine; INT.A = intercostal artery; INT.V = intercostal vein; INN.A = innominate artery; INT.J = internal jugular vein; L.A = laryngeal artery; L.L.L = left lobe of liver; M.S = median sacral vein; the artery of the same name is immediately to the left of it; O.A & V = ovarian artery and vein; P.A = pulmonary artery; P.M = posterior mesenteric artery; P-C = post-caval vein; POS.EP = posterior epigastric artery; POS.F.V = posterior facial vein; R = rectum; T = trachea; V.A = vertebral artery. The pre-caval veins are not lettered, but they are the two veins entering the heart from above and formed by the union of BR.V and EX.J.V.

Rabbit. The **dorsal aorta** (Fig. 28, DO.AO), the main artery of the body, arises from the left ventricle, whence, passing anteriorly, it turns over to the left in the form of an arch. The arch is called the **aortic arch** (Fig. 28, AO.A); and since in all mammals it turns towards the left of the body, it is further called a **left aortic arch**, to distinguish it from that of birds, which always turns towards the right. In both

classes of animals right and left arches exist in the embryonic stage, as in fishes, reptiles, and Amphibia, but in mammals the right side of the second branchial arch (fourth aortic arch) almost completely disappears, the left persisting as the aorta; in birds it is vice versa, i.e. the left disappearing and the right persisting.

The aortic arch, turning to the left, reaches the dorsal surface of the body, where it runs along the vertebral column as the **dorsal aorta** (DO.AO) to the posterior end of the trunk; it here bifurcates to form the **common iliac arteries** (CM.I), which give rise to the **internal** (INT.I) and **external** (EX.I) **iliacs**, the latter of which, when it reaches the leg, is known as the **femoral artery** (F.A). At the point of bifurcation there is given off a **median sacral (caudal) artery** (M.S) that extends along the tail. The **dorso-lumbar arteries** (D-L.A) usually arise from the iliacs, but sometimes from the aorta, a little way behind the genital arteries. They supply the muscles of the dorsal wall of the lumbar region. The **posterior epigastric arteries** (POS.EP) arise from the iliacs, just within the ventral abdominal wall, along which they course.

The Aortic Arch and its branches (Fig. 28, AO.A). In the rabbit the two **common carotids** (C.C.A) both arise from the **innominate artery** (INN.A), which is the first branch given off from the aorta; the **left common carotid** arises from the innominate at its origin, so close to the aorta that it appears to have an independent origin from that, while the **right common carotid** arises as the anterior of two branches derived from the bifurcation of the innominate. The posterior branch forms the **right subclavian artery** (BR.A), while the **left subclavian artery** arises from the crest of the arch; and at a short distance from their origin both arteries give off a **vertebral artery** (V.A), which runs through the vertebrarterial canal of the cervical vertebræ to reach the brain. Both subclavians are continued into the arm as the **brachial artery** (BR.A), which divides at the proximal end of the fore-arm into **ulnar** and **radial** branches.

Branches of the Dorsal Aorta. The **cœliac artery** (Fig. 28, CŒ) arises from the aorta just behind the diaphragm (D), and divides into three main branches: the **gastric artery** (GA) supplying the ventral wall of the stomach, the **hepatic artery** (H) supplying the liver and gall-bladder, and the **duodenal artery** (D) supplying the proximal part of the duodenum and dorsal wall of the stomach. The **splenic artery** (SP), supplying the spleen, arises near the origin of the cœliac. The duodenum (DU), pancreas, ileum (IL), colon, and cæcum (CÆ)

are supplied by numerous branches, derived from the division of the **anterior mesenteric artery** (ANT.M), which arises from the aorta a little way behind the cœliac artery. The **renal arteries** (RE.A) are paired, and arise right and left from the aorta, the left one a little more posteriorly than the right, and pass directly to the kidneys, which they supply. The genital arteries, **spermatic artery** in the male and **ovarian artery** (O.A) in the female, arise a little way behind the renal arteries ; thence the spermatic artery passes backwards to the testes, and the ovarian artery outwards to the ovaries ; both arteries are paired. The hinder portion of the rectum (R) is supplied by a very small artery, the **posterior mesenteric** (P.M), which arises from the posterior end of the aorta. The arteries arising from the bifurcation of the aorta have already been described (ante, p. 100).

THE VENOUS SYSTEM.

Dogfish. The venous system of the dogfish may be considered under three heads : i.e. (1) the **Systemic** ; (2) the **Hepatic-Portal** ; (3) the **Renal-Portal.**

Systemic. This consists mainly of capacious sinuses returning the blood by the **cardinal veins** or **sinuses** (Fig. 29, ANT.CA.S & POS.CA.S) from the kidneys, brain, and the body generally to the sinus venosus of the heart (Fig. 29, S.VE) through the **Cuvierian veins** or **ducts** (D.C), which enter it on either side at its lateral angles. The **posterior cardinal veins** or **sinuses** arise between the hinder portion of the kidneys, from which they receive blood by numerous small **efferent renal veins** (E.R.V) ; at first the cavities of the two sinuses are only partially separated from one another, their inner walls being very incomplete and much fenestrated, but a little way forward the two cavities become distinct, although the veins run in contact with each other in the middle line. In the region of the œsophagus they dilate into capacious cavities, which again become connected with each other by perforations in their inner walls ; at the anterior extremity of the cœlom they narrow somewhat suddenly, and open on either side into the **Cuvierian veins**, but just before doing so each sinus receives a **subclavian vein** (SUB.V) returning blood from the pectoral fins. The **lateral line vein** (L.L.V) is situated in the lateral body-wall, immediately beneath the skin ; it arises from the cloacal region (C.V), and receives blood from the cloaca, tail, and pelvic fins (P.V), and opens into the posterior cardinal sinus a little way behind the point where that receives the subclavian vein. The lateral line vein is

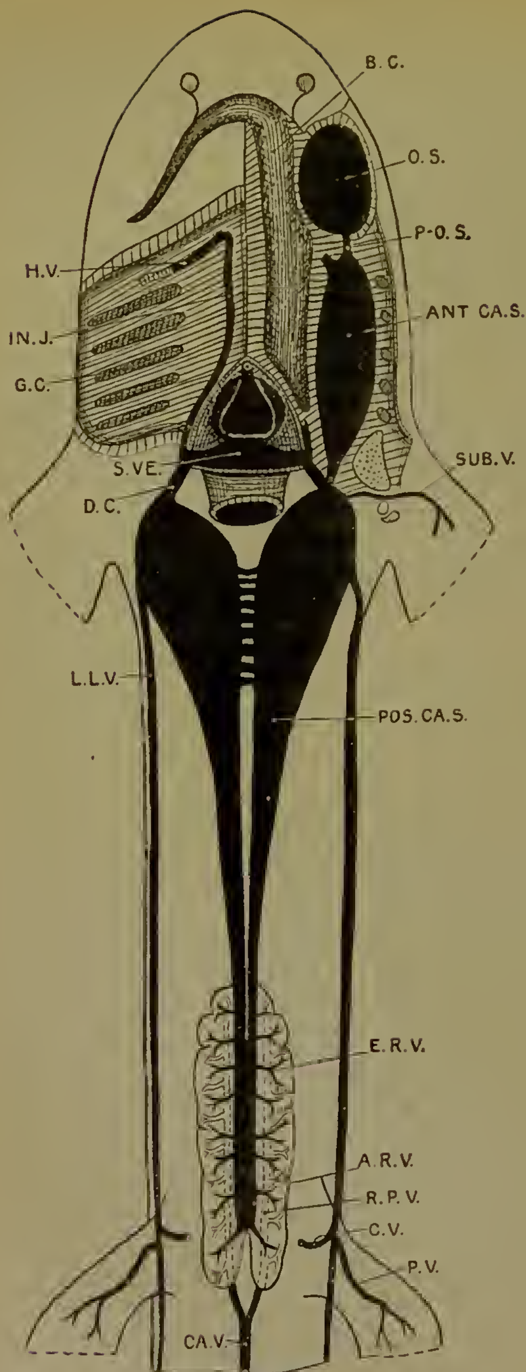


FIG. 29. Ventral dissection of Dogfish (*Scyllium*), to show main systemic venous channels and the renal-portal system. For hepatic-portal system, see Fig. 42. The pectoral and pelvic girdles, ventral body-wall and viscera, together with the mesonephros, have been removed. On the left, the floor and part of the roof of the mouth and the gill-arches have been cut away to show the anterior cardinal sinus. On the right, the skin and most of the muscles in the floor of the mouth have been dissected away, to show the hyoidean vein. ANT.CA.S = anterior cardinal vein; A.R.V = afferent renal vein; B.C = buccal cavity; C.V = cloacal vein; CA.V = caudal vein; D.C = Cuvierian duct or vein; E R.V = efferent renal vein; G.C = gill-cleft; H.V = hyoidean vein; IN.J = inferior jugular sinus; L.L.V = lateral line vein; POS.CA.S = posterior cardinal sinus; P-O.S = post-orbital sinus; P.V = pelvic vein; R.P.V = renal-portal vein; SUB.V = subclavian vein; S.VE = sinus venosus. Just behind the sinus venosus the cut end of the œsophagus can be seen.

interesting, since it is situated immediately beneath the skin, and runs a course which is identical with that of the lateral fin-folds represented in a vestigial condition in the embryos of Elasmobranchs, and to a less extent in amphibians. These fins very probably existed in a well-developed and functional condition in the ancestors of Vertebrates, and the lateral line vein was probably connected with their blood supply; and if this be so, the vein represents the last and most persistent vestige of these primitive fin-folds, its persistence being explained by the fact that it is still of some utility in the circulation. If this interpretation of its nature be correct, its identity with the anterior abdominal vein of the frog (post, p. 108) is of the highest interest, and more especially so since the posterior epigastric vein of the rabbit and the vesico-prostatic venous plexus of man—remnants of the allantoic or umbilical veins in the embryo of both—are embryologically the corresponding vessel to the anterior abdominal of the frog, and, therefore, to the epigastric or lateral line vein of the dogfish; so that, as far as it goes, it furnishes evidence in favour of believing that the rabbit and man are descended from fin-bearing ancestors [1].

The **anterior cardinal sinus** (ANT.CA.S) lies dorsally to the gill-arches, and opens into the Cuvierian vein by a small aperture close to that of the posterior cardinal sinus. Anteriorly it commences at the orbit in which the eye lies, and that is known as the **orbital sinus** (O.S); this communicates by a narrow passage, the **post-orbital sinus** (P-O.S), with the main channel of the anterior cardinal sinus lying above the gill-arches. The groove at the bottom of the auditory capsule, and represented in Fig. 17, is that in which the post-orbital sinus is lodged. The orbital sinuses of either side are in connexion with each other by means of a tubular canal, the **inter-orbital sinus** (Fig. 17), which pierces the cartilaginous base of the skull in the posterior region of the orbit. The **inferior jugular sinus** (IN.J) is a small one running round the outer wall of the pericardium and opening into the Cuvierian vein; anteriorly it runs forward in the floor of the mouth and joins another sinus running along the hyoidean arch, called the **hyoidean sinus** (H.V), which becomes connected with the anterior cardinal sinus. The small vein cut off short (on the reader's right of the figure), just behind the entrance of the post-orbital sinus into the anterior cardinal sinus, is that of the hyoidean vein as it enters the cardinal sinus.

The blood from the liver is returned direct to the sinus venosus by

[1] Cf. chap. vi, 'Development of the Branchial Clefts.'

a wide confluent paired sinus, the **hepatic sinus** (Fig. 25, HEP.S), the median septum of which is very much fenestrated ; the sinus opens into the posterior chamber of the heart by two small apertures, which are situated in the posterior wall of the pericardium.

The hepatic-portal system. This returns the blood from the alimentary canal to the liver, and is composed of several factors, which, arising from different portions of the canal, ultimately unite in a single large vein, the **hepatic-portal vein** (Fig. 42, H-P.V), which carries the blood direct to the liver. The factors of the portal vein are : the **superior mesenteric vein** (Fig. 42, S.M.V), returning blood from the large intestine (C) and rectum (R) ; the **lieno-gastric vein** (L-G.V), returning blood from the posterior end of the stomach and the spleen ; and the **anterior gastric factor** (A.G.F), returning it from the anterior portion of the stomach. The lieno-gastric factor enters the superior mesenteric, which, passing through the pancreas (P), receives the anterior gastric factor and forms by their union the **hepatic-portal vein** (H-P.V). Just before entering the liver substance the portal vein divides into two branches, one of which enters the left (L.L) and the other the right lobe (R.L) of the liver, where they break up into a series of capillaries (Fig. 25, HEP.P.V) ; these subsequently unite within the substance of the liver to form veins, which ultimately open into the hepatic sinus (Fig. 25, HEP.V). The blood that flows through the wall of the alimentary canal has, therefore, to pass through two sets of capillaries before reaching the heart, i. e. the capillaries in the wall of the alimentary canal itself and those in the substance of the liver. The second system of capillaries, with its associated afferent and efferent veins, is called a **Portal System**, and since it is located in the liver, it is distinguished as the hepatic-portal system ; the vein that connects the portal capillaries with those of the alimentary canal is called the **hepatic-portal vein** (Plate I, Fig. 3).

The renal-portal system. The **caudal vein** (Fig. 29, CA.V), running in the hæmal arches of the caudal vertebræ, and returning blood from the tail, divides into two branches, each of which is called a **renal-portal vein** (R-P.V), a little posterior to the kidneys ; each branch (R.P.V) penetrates the substance of the metanephros (kidney), and runs forward along the inner border of either kidney (metanephros), giving off a series of small **afferent veins** (A.R.V) which break up into capillaries in the kidney substance and ramify over the renal tubules ; these are again gathered into small **efferent veins** (E.R.V) that open into the hinder portion of the posterior cardinal sinus. The blood

carried to the tail by the caudal artery passes through its first set of capillaries in the tissues of the tail, thence by the caudal vein it reaches the **renal-portal veins** (R.P.V) which carry it to the second set of capillaries in the kidney substance. This second set of capillaries with the renal-portal veins constitute a **renal-portal system.**

A renal-portal system is found in all fishes, amphibians, reptiles, and traces of it in birds; but it has disappeared in all the Mammalia, with the exception of the embryos of the most primitive mammal (*Echidna*), in which traces only have been found (Plate I, Figs. 1, 2, 3).

Frog. The veins of the frog may be conveniently considered under four heads:—the **Systemic, Hepatic-Portal, Renal-Portal,** and **Pulmonary Systems.**

Systemic system. The embryonic condition of this system of veins in the frog is essentially the same as that in the adult dogfish. But by the time of the metamorphosis of the tadpole certain important changes have taken place, and the anterior cardinals of the tadpole have become converted into the jugular veins (Fig. 30, E.J) of the frog; the posterior cardinals have for the most part disappeared, but their hinder portions merge and give rise to the renal portion (that part between the kidneys) of the post-caval vein (PO.C), while occasionally their anterior portion, sometimes of the left and sometimes of the right vein, may persist and be represented by either a left or right, or both, **azygos veins**, and in some amphibians (*Bombinator*) this portion always persists. The anterior or hepatic portion (the part that passes through the liver) of the post-caval is derived from the right omphalo-mesenteric (the trunk formed by the union of the vitelline and sub-intestinal vein [1]), while the middle portion connecting it with the posterior part is independently formed. Thus the post-caval vein (Fig. 30, PO.C) of the frog is in part formed from the posterior cardinal and omphalo-mesenteric of the tadpole, and in part arises independently.

The precavals (Fig. 30, P.C) of the frog are the persistent Cuvierian veins of the tadpole, the transverse direction of which has become obliquely longitudinal by the backward displacement of the heart.

In the adult frog all the systemic veins enter three main trunks, i. e. the **post-caval** (Fig. 30, PO.C) (**posterior vena cava**) and the two **precavals** (P.C) (**anterior venæ cavæ**). The veins entering the

[1] The vitelline veins come in from the yolk-mass, and the sub-intestinal is the primitive vein of the first-formed gut. The latter unites with one of the two former to form the omphalo-mesenteric.

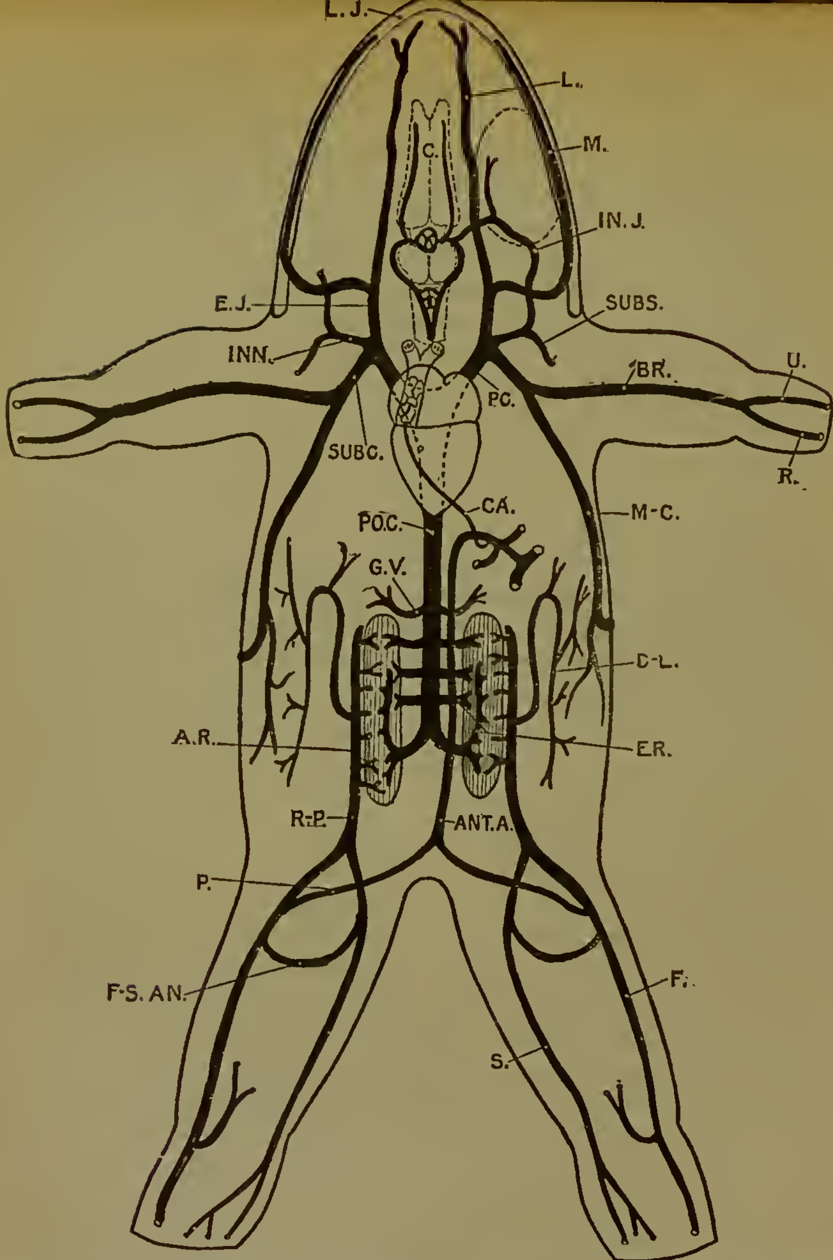


FIG. 30. Ventral dissection of the Frog (*Rana*), to show the principal veins of the systemic and renal-portal systems. The pectoral and pelvic girdles and the ventral body-wall have been removed, as well as the viscera. For the sake of completeness, the outlines (dotted line) of the brain and the veins connected with it have been represented, and are supposed to be seen through the floor of the mouth and the base of the cranium ; the floor of the mouth is uninjured and the lingual and mandibular veins lie in it. The oval dotted line is the orbit of the eye. ANT.A = anterior abdominal vein ; A.R = afferent renal veins ; BR = brachial vein ; C = cerebral hemispheres of brain ; CA = cardiac vein ; D-L = dorso-lumbar vein ; E.R = efferent renal veins ; E.J = external jugular vein ; F = femoral vein ; F-S.AN = femoro-sciatic anastomosis ; G.V = genital vein ; INN = innominate vein ; IN.J = internal jugular vein, completely represented only on the left side ; L = lingual vein ; L.J = lower jaw (mandible) ; M = mandibular vein ; M-C = musculo-cutaneous vein ; P = pelvic vein ; P.C = precaval vein ; PO.C = post-caval vein ; R = radial vein ; R-P = renal-portal vein ; S = sciatic vein ; SUBC = subclavian vein ; SUBS = sub-scapular vein ; U = ulnar vein. The triangular space enclosed by dotted lines, behind the heart, is the sinus venosus.

latter return the blood from the head, brain, and fore-limbs; the principal of these veins are—(1) the **external jugular** (Fig. 30, E.J), formed by the union of the **lingual** (Fig. 30, L) and the **mandibular** (M) **veins**, the former of which returns blood from the tongue and hyoid muscles and the latter from the sub-maxillary and associated muscles; (2) the **innominate vein** (Fig. 30, INN), formed by the joining of the **internal jugular** (IN.J) and **subscapular** (SUBS) **veins**, the former returning blood from the brain and orbit of the eye, and the latter from muscles associated with the shoulder girdle; (3) the **subclavian vein** (SUBC) is formed by the union of the **brachial** (BR) and **musculo-cutaneous** (M·C) **veins**, the former of which brings blood from the arm and the latter from the muscles and skin of the head and body. Each of these three veins is thus composed of two factors, and the three main trunks by their union form the **precaval vein** (P.C), right and left as the case may be, which enters the sinus venosus at one of its two anterior angles, the precaval of the other side entering at the other angle.

The **post-caval vein** (PO.C) arises between the kidneys by the confluence of the **efferent renal veins** (E.R); the **genital veins** (G.V), **spermatic** in the male and **ovarian** in the female, enter it just in front of the kidneys. Passing forward in the middle line it pierces the liver and receives two **hepatic veins** (not represented in the figure), immediately after which it enters the sinus venosus at its apex (posterior angle).

Renal-portal system. The largest venous trunks of the leg are the **femoral** (Fig. 30, F) and **sciatic** (S) **veins**; the femoral is the larger of the two, and upon reaching the floor of the pelvis divides into a dorsal **iliac** and a ventral **pelvic vein** (Fig. 30, P); the former unites with the sciatic vein to form the **renal-portal vein** (R-P), which runs forward along the outer border of the kidney, while the latter turns towards the middle line and meets its fellow of the other side, with which it unites to form the **anterior abdominal** (**epigastric**) **vein** (ANT.A). The renal-portal vein gives off a series of **afferent renal veins** (AF), which break up into very large capillaries that spread out over the renal tubules and ultimately join the **efferent renal veins** (E.R); these are mainly confined to the ventral surface of the kidney, and open into the post-caval (PO.C). The branches derived from the renal arteries break up and form a series of capillary tufts, each of which is contained in a Malpighian capsule [1], emerging

[1] See chap. vii, 'Urino-genital Organs.'

from which the capillaries abruptly enter an adjacent venous anastomosis (*for diagrammatic representation see coloured Plate* I, Fig. 2). Thus the capillaries derived from the venous channels, i. e. the afferent renal veins, spread out over the renal tubules, while those derived from arterial sources form tufts within the Malpighian capsules (enlarged and indented terminations of the renal tubules). This is a fact of great importance to the physiologist, since by ligaturing either the dorsal aorta or the renal-portal vein, in conjunction with the injection of certain pigments, it has been possible to determine the nature of the respective functions of the Malpighian capsules and the tubules. And it has been shown that the capsules only allow water to filter through, while the tubules excrete the urea and hippuric acid.

The **dorso-lumbar veins** (D-L) receive the blood from the dorsal wall of the lumbar region and empty it into the renal-portal vein.

Anterior abdominal vein (Fig. 30, ANT.A & Fig. 43, AN.AB.V). This passes forward in the ventral mesentery in the middle line of the ventral abdominal wall, and at the level of the liver it divides into three branches, two of which enter that organ, one to the left and the other to the right lobe, while the third, the ramus descendens, opens into the hepatic-portal vein. Just before its division into three it receives a small **cardiac vein** (Fig. 30, CA) that returns blood from the wall of the truncus arteriosus, which is the only portion of the frog's heart that possesses blood-vessels in its wall. Immediately upon its formation by the union of the two pelvic veins (P), the anterior abdominal vein receives another, the **vesical vein**, which returns blood from the bladder (ante, p. 103). In the early stages of its development the anterior abdominal vein is *paired*, and is connected anteriorly, not with the liver, but with the sinus venosus. Later, the two veins unite at their hinder ends, and subsequently in front of this, the right one of the pair disappears, the left persisting as the adult vein; still later it loses its primary connexion with the sinus venosus and acquires a secondary one with the hepatic-portal vein. In its primary paired nature, its connexion with the bladder (cloacal region) on the one hand and with the sinus venosus on the other, it is in almost complete agreement in its anatomical relations with the lateral line veins of the dogfish (cp. p. 103).

Hepatic-portal system. This system returns the blood from the whole length of the alimentary canal and spleen to the liver

through the hepatic-portal vein, as well as a portion of the blood from the hinder extremities through the anterior abdominal vein.

Hepatic-portal vein (Fig. 43). This is formed by the union of the **gastric vein** coming from the stomach (ST), pancreas (PA), and duodenum (DUO); the **intestinal vein** coming from the ileum (IL) and a portion of the duodenum; the **splenic vein** returning the blood from the spleen (SPL); and the **hæmorrhoidal veins** coming from the large intestine (CO). The **hepatic-portal vein** enters the left lobe (L. LO) of the liver, but it is connected with the right lobe (R.LO) by the descending branch of the anterior abdominal vein. In Fig. 30 the anterior termination of this vein is shown as a H-like figure somewhat obliquely placed: the lower and thicker limb of the H is the hepatic-portal vein, the upper cut end of which enters the left lobe of the liver, while the lower cut end is that of the main trunk of the vein; the upper limb of the H represents the right and left branches of the anterior abdominal vein, which respectively enter the right and left lobes of the liver; the cross-piece of the H is the descending branch of the anterior abdominal vein mentioned above, and by means of which the blood of the portal vein enters the right lobe of the liver.

Pulmonary veins. These are two in number, one from either lung. They arise from the inner border of the lung, and running up above the corresponding precaval veins they unite to form a common trunk, the **common pulmonary vein**, which enters the dorsal wall of the left auricle at its anterior inner corner (Fig. 23, B, PUL.VE). It returns oxygenated (arterial) blood from the lungs.

Rabbit. The venous system of the rabbit may be considered under the following heads:—**Systemic, Pulmonary,** and **Hepatic-Portal Systems.** Unlike the dogfish or the frog, a renal-portal system is absent.

Systemic. The venous blood of the body and the liver is returned directly to the right auricle by the two precaval and the single post-caval veins, since the sinus venosus no longer exists as a separate structure, but has become incorporated with the auricle and the base of the caval veins.

Precaval or Anterior Venae Cavae veins (Fig. 28). The precaval veins return the blood from the head, neck, thorax, and fore-limbs, and are formed by the union of the following factors: (1) **External jugular vein** (EX.J.V), which returns blood from the head and ears; it is formed by the union of two other factors, i. e.

anterior (ANT.F.V) and **posterior** (POS. F.V) **facial veins.** (2) **Internal jugular vein** (INT.J), which returns blood from the brain and enters the external jugular close to its union with the subclavian. (3) The **subclavian vein** is the thoracic continuation of the **brachial vein** (BR.V), returning blood from the arm and shoulder. By the union of the subclavians and external jugulars of either side the **precaval veins** are formed; these pour the blood into the right auricle. (4) **Intercostal vein**, returning blood from the five anterior intercostal spaces. (5) **Internal mammary vein**, opening directly into the precaval and returning blood from the chest wall and mammary glands.

The precavals (anterior venæ cavæ) in the rabbit, as in the frog, are the persistent Cuvierian veins of the embryo. The last remnant of the embryonic right posterior cardinal of that side persists as a small, nearly median vein, the **azygos vein** (AZ.V), which conveys blood from the posterior intercostal spaces of both sides of the thorax to the right precaval. The left posterior cardinal completely disappears.

Post-caval or **Posterior Vena Cava** (Fig. 28, P-C). The post-caval is a large median vein running by the side of the aorta along the ventral surface of the vertebral column. It arises in the posterior end of the abdomen by the union of the **external** (EX.I.V) and **common iliac veins** (CM.I.V); the latter in its turn is formed by the union of the internal iliac veins (INT.I). These return blood from the hinder extremities, from the thigh and bladder, and in the female from the uterus; the external iliac vein is the direct continuation of the **femoral vein** (F.V) which runs along the inner border of the thigh. The blood from the genital glands (ovaries or testes) is returned to the post-caval through a pair of veins, **ovarian** (O.V) or **spermatic veins** as the case may be, a little way in front of its union with the iliac veins. The **renal veins** (RE.V) enter the post-caval at different levels, the right one, which is the shorter of the two, opening into it more anteriorly than the left. While passing through the liver the post-caval enlarges considerably, and receives four hepatic veins; these open into the post-caval, and carry to it the blood that is brought to the liver by the hepatic-portal vein and hepatic artery. While piercing the diaphragm it receives a few small veins from the dorsal surface of that. Its opening into the right auricle has already been described (ante, p. 88).

Hepatic-portal system. This returns the blood from the capil-

laries in the walls of the alimentary canal, and is formed of the several factors arising from the different portions. The factors which take their origin from the cæcum (CÆ.F), colon (C.F), the whole of the small intestine (IL.F), and from a portion of the rectum, unite to

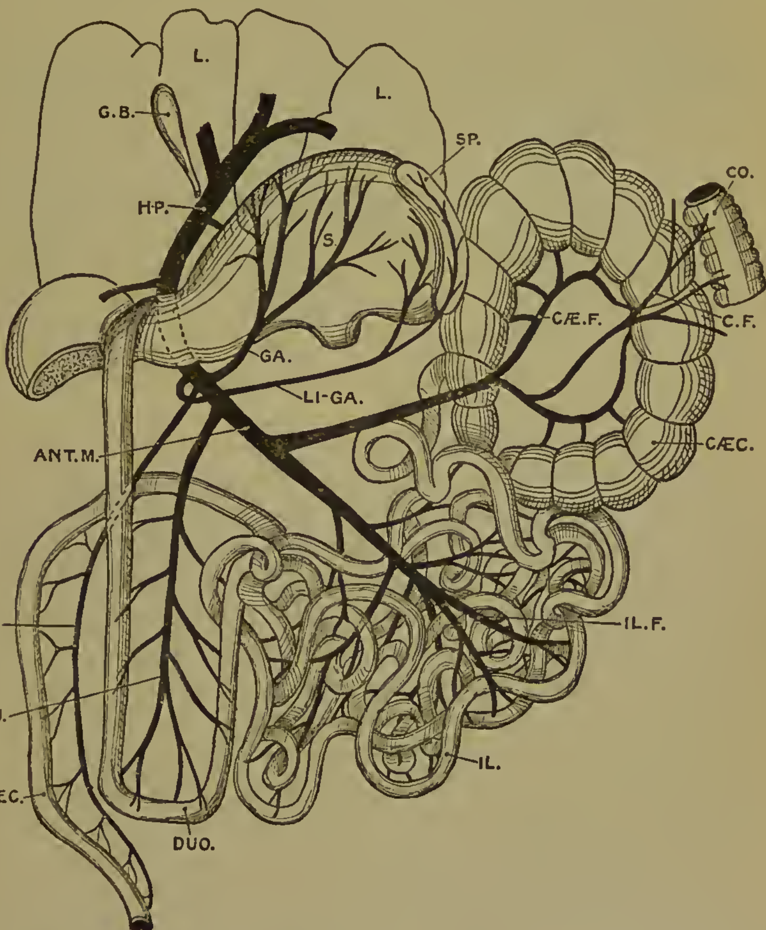


FIG. 31. The hepatic-portal system of the Rabbit (*Lepus*). The cæcum and colon have been turned over to the left, and the stomach forwards. ANT.M = anterior mesenteric factor; CÆC = cæcum; CÆ.F = cæcal factor; C.F = colic factor; CO = colon; DU = duodenal factor; DUO = duodenum; GA = anterior gastric factor; G.B = gall-bladder; H-P = hepatic-portal vein; IL = ileum (small intestine); IL.F = ileal factor; L = liver; LI-GA = lieno-gastric factor; POS.M = posterior mesenteric factor; REC = rectum; S = stomach; SP = spleen.

form the **anterior mesenteric vein** (ANT.M); this then receives the **lieno-gastric** (LI.GA) vein which returns blood from the stomach and spleen, the **anterior gastric factor** (G.A) that returns blood from the

dorsal, and in part ventral, surface of the stomach, the **duodenal vein** (DU) that brings blood from the pancreas and duodenum, and the **posterior mesenteric vein** (POS.M) which comes from the hinder portion of the rectum. The union of all these factors form the **hepatic-portal vein** (H-P), which passes immediately towards the liver and sends a branch into each of its lobes (L).

Pulmonary veins. These return oxygenated (arterial) blood from the lungs to the left auricle by two veins from either lung, which enter the auricle separately (Fig. 24).

The Arterial Arches compared.

In the adult dogfish there are four arterial arches, which are paired, and arise right and left from a median artery coming directly from the heart. In the frog this number is reduced to three, and these have a very different distribution. In the rabbit they are reduced to a yet greater extent, for there are but two, and one of these is represented on the left side of the body only.

The study of embryology reveals the fact that all Vertebrates, *Amphioxus* excepted, in the earlier periods of their development, pass through a stage when right and left arterial arches are present as in the dogfish; and if this is so, it becomes necessary to inquire as to how far those of the adult are derived by metamorphosis or evolution from those of the embryo, or whether they arise, *sui generis*, as entirely new structures. No chapter in the remarkable record of Vertebrate development—that relating to the origin of the primitive kidney perhaps excepted—is so interesting as that which pertains to the embryological metamorphosis of the arterial arches, by which it is demonstrated that the adult condition of them in all mammals whose development is known, man included, arises from an origin which, as far as their relation and distribution are concerned, is veritably that of a fish; and indeed is even more, for in virtue of the presence in human and rabbit embryos of the **mandibular** and **hyoidean arches**, it is that of an *embryo* fish.

In the embryos of all Vertebrates, *Amphioxus* excepted (Fig. 32), there are present six arterial arches[1], which are numbered from before backwards, and are named in this order as follows:—(1) **mandibular**

[1] In the chick and man, one of the arches, probably the fifth, is absent. It probably exists, like that in the rabbit, in a transient and very imperfect condition, and possibly has been overlooked.

arterial arch (Fig. 32, M); (2) hyoidean arterial arch (H); (3–6) branchial arterial arches (Fig. 32, 1.B–4.B). Of these arches, the

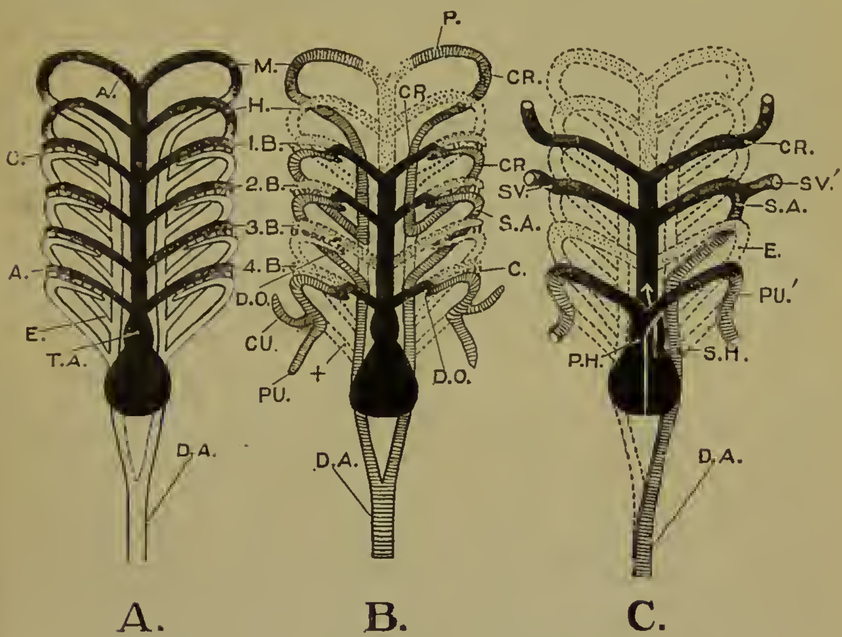


FIG. 32. Semi-diagrammatic representation of the metamorphosis of the arterial arches in the Dogfish (A), Frog (B), and Rabbit (C).—A. Embryo dogfish; the mandibular and hyoidean arches disappear, but otherwise the diagram will serve for the adult dogfish as well. In B and C the broken lines represent the retrogressive efferent portions and the dotted stipple the retrogressive afferent portions of the arches. The cross stipple represents the efferent portion of the arches which have persisted or of parts which arise as diverticula of them. In the mandibular and hyoidean arches, and in the rabbit the branchial arches also, the afferent portion is *directly* continuous with the efferent, and not connected indirectly through gill-capillaries, for in the embryos of reptiles, birds, and mammals, although there are gill-clefts, there are no gill-filaments and hence no gill-capillaries. In the embryo frog (tadpole) the first gill-capillary (D.O) in each arch is very wide and later becomes the connexion by which the efferent portion becomes directly continuous with the afferent (note the last arch on left-hand (the reader's right) side in B in which the index line of D.O points directly to this enlarged first capillary). In the diagram C, the mandibular and hyoidean arches are represented as having completely disappeared; they do so as arches, but portions of them persist as explained in the text. A = afferent portion of arterial arch; B = branchial arches; C = the gill-capillaries connecting afferent and efferent portions; CR = carotid arch; CU = diverticulum from efferent portion of fourth branchial arch to form the cutaneous artery; D.A = dorsal aorta; D.O = direct passage (enlarged first gill-capillary) between afferent and efferent portions; E = efferent portion of arch; H = hyoidean arch; M = mandibular arch; P = pharyngeal artery; P.H = pulmonary half of truncus arteriosus; PU = diverticulum from efferent portion of fourth branchial arch to form pulmonary artery; PU′ = pulmonary artery; S.A = systemic arch; SV = right subclavian vein; SV′ = left subclavian vein; S.H = systemic half of truncus arteriosus; T.A = truncus arteriosus; + = retrogressive portion of fourth efferent branchial arch.

mandibular and hyoidean for the most part disappear in the dogfish, frog, and rabbit; while in the dogfish the posterior four, i.e. first, second, third, and fourth branchial arterial arches (1.B–4.B), persist unaltered

throughout life, and in the tadpole of the frog they exist in only a slightly modified condition up to the period of development of the lungs, after which, by the retrogression or modification of certain of them, the adult condition is reached.

Frog. The **pharyngeal artery** (branch of the external carotid artery) of the adult is the last remnant of the mandibular arterial arch (Fig. 32, B, P), and the **hyoidean vein** of the tadpole is the only vestige of the hyoidean arterial arch. For all practical purposes, we may say that the first and second arches almost wholly disappear in the frog.

The first branchial arterial arch. During the time that the tadpole is breathing by gills, the afferent branchial arteries are connected with the corresponding efferent ones by two channels, i.e. the capillaries (Fig. 32, B, C) of the gill, and a direct passage (Fig. 32, B, D.O) situated at the ventral end of the efferent vessel (E); so that blood in its course from the afferent to the efferent arteries must first pass over the aperture of the direct passage before reaching the capillaries of the gill. At first the direct passage is very small, and by far the greater portion of the blood reaches the efferent vessel, and thence to the aorta by passing through the capillaries, but at about the time of the metamorphosis, when the lungs are fully developed, the direct passage widens and less blood passes through the capillaries of the gill, and an ever-increasing quantity through the widened passage. As a result, the capillaries of the gill and the gill itself atrophy, together with that portion of the afferent artery that lies beyond the direct passage. Soon after this, the portion of the aorta between the first and second efferent branchial arteries (Fig. 32, B, D.A) suffers obliteration of its lumen and ultimately becomes a mere thread, so that the blood can no longer travel backwards to the aorta, but only forwards. The vessel thus formed from the first branchial arterial arch and the portion of the aorta lying in front of it becomes the **carotid artery** of the adult (CR). The second branchial arterial arch undergoes similar changes, by which the capillaries of the gill and the gill itself atrophy, and the blood passes direct to the efferent vessel, which retains a permanent connexion with the aorta, and so forms the **systemic arch** of the adult (S.A). The third branchial arterial arch disappears altogether. The fourth branchial arterial arch undergoes the same changes as the second and third, but previously a small backwardly directed diverticulum (PU) arises from it which ultimately acquires a connexion with the lung, and at a later period becomes

the **pulmonary artery**. From the root of the pulmonary diverticulum there also arises another (CU) which is directed dorsally and laterally and becomes the **cutaneous artery**. At the time of the metamorphosis, the portion (+) of the efferent vessel between the origins of the pulmonary and cutaneous arteries and the aorta begins to lose its cavity and later becomes a solid cord, so that the whole of the blood passes from the fourth arch to the lungs and skin and no longer to the aorta. The fourth branchial arterial arch (sixth aortic arch) thus becomes the **pulmo-cutaneous arch** of the adult frog.

Rabbit. The mandibular and hyoidean aortic arches become converted into the arteries of the floor of the mouth and tongue, i. e. branches of the external carotid artery. As in the frog, the third aortic arch (first branchial arterial arch) becomes the **carotid arteries** (Fig. 32, C, CR), (external and internal).

The fourth pair of aortic arches (second branchial arterial arch) become the **systemic arches** (Fig. 32, C, S.A), which retain their continuity with the dorsal aorta. At first the two arches (right and left) are of equal size, but from a very early period the left becomes much the larger of the two and ultimately forms the **aortic arch**, the greater part of the right disappearing, some portion of it remaining as the right subclavian artery (Fig. 32, C, SV). The left subclavian artery (SV′) arises as an outgrowth of the aortic arch. The apparently fifth aortic arch, but in reality the sixth, forms the **pulmonary arches** (Fig. 32, C, PU′). In the frog, the fifth aortic arch (third branchial arterial arch), though at first equally well developed with the others, ultimately disappears. In the rabbit, this arch never reaches a great degree of development, and only traces of it are found; and hence it was previously overlooked, and the sixth arch was therefore counted as the fifth. This observation shows that the pulmonary arches in the frog and rabbit are corresponding structures, i. e. arise from the same embryonic arch.

Up to this stage, the blood passing from the single ventricle may enter the pulmonary or systemic arches indifferently, since both these open into a common truncus arteriosus, as is the case throughout life in the frog. At the twelfth to the fifteenth day, however, the ventricle becomes divided by a ventricular septum (represented by a median white line in the heart of Fig. 32, C), into right and left halves; and shortly after this, a longitudinal septum arises in the truncus arteriosus, first commencing between the roots of the systemic and pulmonary arches, and extending backwards in a somewhat spiral fashion, until

TABULATION OF CHIEF DIFFERENCES IN THE HEART AND AORTIC ARCHES OF:—

	Dogfish.	Frog.	Rabbit.	Chick.
Sinus venosus.	Posterior to atrium.	Dorsal to atrium.	Incorporated with wall of right auricle and base of the caval veins.	As in rabbit.
Atrium.	Dorsal to ventricle and single-chambered.	Anterior to ventricle and divided into two auricles.	Anterior to ventricle and divided into two auricles. Each auricle produced into an auricular appendage.	As in rabbit.
Ventricle.	Single chambered.	Single chambered.	Divided into left and right ventricles: the left thicker walled.	As in rabbit.
Relative arrangement.	Parts arranged in an S-shaped loop.	Primitive arrangement lost in course of development.	As in frog.	As in frog.
Nature of blood.	Contains wholly venous blood.	Venous blood in right auricle and arterial in left, which slightly mix in ventricle.	Venous blood in right side of heart and arterial in left; the two streams never mix.	As in rabbit.

Truncus arteriosus.	Consists of a conus and bulbus arteriosus with semilunar valves in two transverse rows.	Consists of a conus (pylangium) and bulbus (synangium). Conus contains spiral valve free along one margin.	Becomes divided into two and incorporated with base of pulmonary and systemic arches.	As in rabbit.
Mandibular arch (*1st aortic arch*).	Disappears during development.	Becomes pharyngeal artery of adult.	Form arteries of floor of mouth, which lose all characters as arches and become branches of external carotid.	As in rabbit, but in addition, their dorsal (efferent) portions contribute to formation of carotid artery.
Hyoidean arch (*2nd aortic arch*).	Probably represented in adult by hyoidean vein.	Becomes hyoidean vein of adult.		
1st branchial arterial arch (*3rd aortic arch*).	Retains embryonic relations throughout life.	Becomes **carotid arch.**	Becomes **carotid** (internal and external) **arteries.**	In part forms the root of **common carotids,** and in part that of the **subclavian artery.**
2nd branchial arterial arch (*4th aortic arch*).	As in 1st.	Becomes **systemic arch.**	Becomes **aortic** (*left* systemic) **arch & right subclavian artery.**	Becomes **aortic** (*right* systemic) **arch.** Left side of arch disappears.
3rd branchial arterial arch (*5th aortic arch*).	As in 1st.	Wholly disappears.	Never fully developed and quickly disappears.	Becomes **pulmonary arch** of adult. Probably this arch really represents the sixth.
4th branchial arterial arch (*6th aortic arch*).	As in 1st.	Becomes **pulmo-cutaneous arch.**	Becomes **pulmonary arch.**	Not present. Perhaps represented by the fifth.

it meets and merges with the ventricular septum. The effect of this is to divide the truncus arteriosus into right (or pulmonary) (P.H) and left (or systemic) (S.H) halves, so that the blood passing from the right side of the ventricle can only pass through the pulmonary arch and that from the left through the systemic. At first, this division only affects the internal cavity of the truncus, but it is later followed by an external constriction, which divides the septum and truncus into two, i. e. into pulmonary and aortic arches. Subsequently, upon the retrogression of the *right* half of the systemic arch, the adult condition is attained.

CHAPTER V

NERVOUS SYSTEM

THE nervous system of Vertebrates consists of a **central organ** connected with a **peripheral series** concerned with transmitting stimuli to and from it. The former is constituted by the **brain** and **spinal cord**, and the latter by the **cranial**, **spinal**, and **sympathetic nerves**. The central nervous system and all the sense organs connected with it arise as differentiated portions of the same embryonic layer, the **epiblast**, that gives rise to the skin. Its deeply seated and protected position is a secondary acquirement attained during the course of development. The sympathetic nervous system is a specialized portion of the central system, and arises later than that in the course of development.

The nervous system, including the sympathetic, primitively exhibits evidences of metameric[1] arrangement, which is very distinct along the whole length of the spinal cord and remains so throughout life, but in the posterior portion of the head it is less distinct, and in the anterior portion it is largely hypothetical.

It will be convenient to consider the brain, cranial nerves, spinal nerves, and sympathetic nervous system separately.

THE FUNDAMENTAL FACTS OF THE DEVELOPMENT OF THE BRAIN AND SPINAL CORD.

The brain and spinal cord are primitively of the nature of a simple tube. This tube, called the **neural tube** (Fig. 15, N.C), runs the

[1] By metamerism is understood a serial repetition of organs, or organs arranged segmentally one behind the other.

greater length of the body, and lies dorsad of the notochord, which, as a matter of fact, supports it. In the head region of the body the neural tube is dilated to form the **cerebral vesicle** ; a little later this dilation becomes constricted by two circular furrows into three compartments, all widely in communication, and which are named from before backwards, the **fore-** (Fig. 15, F.B), **mid-** (M.B), and **hind-** (H.B′) **brain**.

Very early in development, owing to the rapid growth of the neural tube, which grows more quickly than the other tissues, the cerebral vesicle becomes bent at right angles (Fig. 15), in such a way that the mid-brain becomes the anterior extremity of the nerve tube. This bend at the mid-brain is called the **cranial flexure**, and is developed in the embryo of all craniate Vertebrates. The brain of the dogfish and that of the frog lose this primitive flexure as development proceeds, so that in the adult the parts of the brain lie in the same plane (Fig. 33). In the brain of the rabbit (Fig. 35) two other flexures are formed as the embryo progresses, i. e. the **cervical bend** (a little behind C.P near extremity of the figure) at the junction of the hind-brain and spinal cord, and the **Varolian bend** (immediately in front of C.P) at the junction of cerebellum and hind-brain. From these three parts, i. e. fore-, mid-, and hind-brain, of the primitive brain arise all the structures that are present in the adult organ, even the most complex. The **cerebral hemispheres** (Fig. 34, L.V) arise as two antero-lateral outgrowths of the fore-brain (T.C) ; the **pineal body** (Fig. 33, EP.B) as an outgrowth of the roof, and the **infundibulum** (Fig. 33, IN) as an outgrowth of its floor. The fore-brain, itself, becomes the **thalamencephalon** (TH) ; the **mid-brain** gives rise to the **optic lobes** (Figs. 34 & 37, OP.LO) ; and the hind-brain becomes the **medulla oblongata** (Fig. 37, MED.OB), the **cerebellum** (Fig. 33, MC′) arising as an outgrowth of the anterior portion of its roof. The ventricles of the adult brain are the persistent and modified portions of the primitive tubular cavity.

The brain of any craniate Vertebrate from fish to man is alike in its earliest embryonic condition, and the only fundamental difference which exists between the adult brain of different Vertebrates is a matter of the relative development of different parts ; there is nothing in the brain of man that cannot be referred to as merely an extension, greater development, or modification of some one of the parts of the primitive brain of the fish.

The Adult Brain.

Dogfish. The brain of the dogfish is specialized in the direction of a great development of the olfactory lobes and the cerebellum (Fig. 36, OL.L & C). This is doubtless correlated with the habits of the animal, which finds its food more by smell than sight, and since the cerebellum has to do with the equilibration of the animal's position, it is always largely developed in fishes, as their normal position is usually one opposed to that which it would assume were the mechanical forces of the surrounding medium alone acting upon it. The greater and more vital to the animal's existence the activities of any organ, the more largely developed is the nerve centre controlling it.

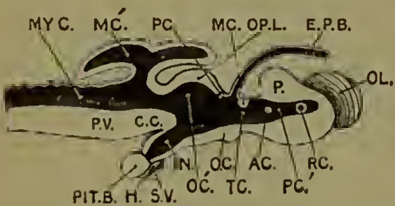


Fig. 33. Median vertical section of the brain of Dogfish. AC = anterior commissure; C.C = crura cerebri; E.P.B = epiphysis or pineal body proper; H = hypophysis; IN = infundibulum; MC = middle commissure; MC′ = metacœle or cavity of cerebellum; MYC = myelocœle; O.C = optic chiasma cut across; OC′ = optocœle or cavity of optic lobes; OL = olfactory lobe; OP.L = optic lobe; P = prosencephalon; PC = posterior commissure; PC′ = prosocœle (rudimentary lateral ventricle); PIT.B = pituitary body; P.V = pons Varolii; RC = aperture of rhinocœle into lateral ventricle; S.V = saccus vasculosus; TC = thalamocœle or third ventricle.

The anterior end of the brain is constituted by the **prosencephalon** (Figs. 36 & 33, P), which is triangular in form and with its base directed forwards; from each antero-lateral corner a large broad outgrowth arises called the **olfactory lobes** (Figs. 36 & 33, OL.L & OL). The prosencephalon exhibits a faint indication of division into paired halves, which, however, is more apparent internally where two cavities, each of which is called a **lateral ventricle** or **prosocœle** (Fig. 33, PC), are developed, one on either side of the median line; these are continuous towards their anterior ends with a cavity that passes into either olfactory lobe, each of which constitutes the **olfactory ventricle** or **rhinocœle**. The lateral ventricles are very small and rudimentary, and in other members of the Elasmobranchii, i. e. the rays, both lateral and olfactory ventricles are absent, the prosencephalon and olfactory lobes being solid throughout.

The posterior portion of the prosencephalon is formed by the primitive (embryonic) fore-brain, which is called in the adult the **thalamencephalon** (Fig. 36, TH), and the cavity of which is known as the **third ventricle** or **thalamocœle** (Fig. 33, TC); the ventricle is roofed over by a vascular membrane, the **choroid plexus**. From the

posterior margin of the dorsal roof of the thalamencephalon there arises a tube-like structure (Fig. 33, E.P.B), which passes upwards and forwards to the membrane covering in the anterior fontanelle of the cranium; it is the remains of an organ more largely developed in reptiles, and among them, very marked and functionally active in *Hatteria*. When fully developed it consists of a ventral stalked portion, the **epiphysis**, arising from the thalamencephalon, and of a more dorsal outgrowth, the **parietal organ**; the latter may lie within the skull or outside it, and remain exposed as in *Hatteria*, or be covered by a scale as in lizards. In many cases, especially in *Hatteria*, the parietal organ presents the microscopic characters of a visual organ, containing a lens, a retina, nerve-cells, and a nerve stalk; it is, moreover, of the nature of a vesicle, the cavity of which is filled with fluid, very much like the posterior chamber of the Vertebrate lateral eye.

The epiphysis is present in all craniate Vertebrates from man downwards, so that their ancestors possessed a 'median eye,' which has now almost disappeared, only persisting in any degree of perfection in the primitive reptile of New Zealand (*Hatteria*).

Behind the thalamencephalon are two ovoidal-shaped portions, the **optic lobes** (Fig. 33 & 36, OP.L. & O.L), which are outgrowths of the primitive mid-brain, and the cavities of which are known as **optocœles** (Fig. 33, OC′). The posterior portion of the brain behind this is constituted by the primitive hind-brain or **medulla oblongata** (Fig. 36, MED.O), sometimes called the **spinal bulb**. The cavity of this is the **fourth ventricle** or **myelocœle** (Fig. 33, MYC), and is roofed over by a choroid plexus. Anteriorly the side walls of the medulla are folded outwards and somewhat upwards to form the **restiform bodies** (Fig. 36, RES.B). From the anterior end of the medulla oblongata a large dorsal outgrowth, the **cerebellum** (Fig. 36, C), arises and stretches forwards over the optic lobes and backwards over the medulla; its cavity, the **metacœle** (Fig. 33, MC′), opens into the fourth ventricle. The two sides of the cerebellum are placed in communication by a strand of fibres that passes across the ventral surface of the medulla, and is called the pons Varolii; it arises in the floor of the medulla during development.

The ventral floor of the thalamencephalon grows downwards and backwards into a pair of prominent oval swellings, the **lobi inferiores**; the outgrowth, as a whole, is known as the **infundibulum** (Fig. 33, IN). Attached to the hinder end of the infundibulum is the **pituitary body**

(Fig. 33, PIT.B), composed of a rounded body of spongy consistency, which is connected with two thin-walled sacs, the **sacci vasculosi**, and upon its ventral median surface there extends a tubular body of unknown significance, the **hypophysis**.

The pituitary body arises as a dorsal invagination of the wall of the stomodæum, which is in its turn an invagination at the anterior end of the embryonic body, and that later gives rise to the buccal cavity. The pituitary body, therefore, though secondarily closely connected with the brain, does not arise as an outgrowth from it.

The prosencephalon, which is the centre whence all voluntary and intelligent actions originate, is in direct connexion with the spinal cord, thence through the spinal nerves with the outer world by means of two tracts of fibres that pass from it along the ventral surface of the medulla and the spinal cord, and are called the **crura cerebri** in the region of the brain, but are known as the **ventral pyramids** when they reach the spinal cord. A little way behind the medulla the ventral pyramids cross each other, or, in technical language, decussate. Hence impulses generated in the right side of the brain pass to the left side of the body and vice versa.

The right and left sides of the prosencephalon, of the thalamencephalon, and of the optic lobes, are connected by transverse tracts of nerve fibres, known respectively as the **anterior** (Fig. 33, AC), **median** (MC), and **posterior** (PC) **commissures**.

Frog. Although the brain of the frog is more advanced than that of the dogfish in virtue of the division of the prosencephalon into two **cerebral hemispheres** (Figs. 37 & 34, CB.H), and the marked development of the lateral ventricles (L.V), yet it is, on the whole, simpler on account of the comparative smallness of the olfactory lobes and the almost insignificant development of the cerebellum. The lateral ventricles are relatively very large and are placed in communication with each other, and with the thalamocœle, or third ventricle, by a small canal called the **foramen of Monro** (Fig. 34, F.M). The **olfactory lobes** (Fig. 37, O.L) are situated directly in front of the cerebral hemispheres, and are in fact the direct continuation of those; they are prolonged forwards to form the **olfactory nerves** (Fig. 37, 1st), and along their whole length are fused to each other by their inner surfaces. The **thalamencephalon** (Fig. 37, TH) is relatively well developed and its roof is formed by a choroid plexus; its ventricle or thalamocœle (Fig. 34, T.C) is relatively spacious. In the larva (tadpole) the epiphysis (pineal organ proper) is continued

forwards and reaches the integument through an aperture in the skull, where an exceedingly small vestige of a parietal organ has been seen. In the adult the epiphysis becomes reduced and lies entirely within the skull-case, but very frequently traces of its previous extra-cranial existence persist in the form of a pigmented spot in the skin, situated between the two eyes, and known as the 'brow-spot.' The **optic lobes** (**mesencephalon**) (OP.LO) are well developed with large ventricles or optocœles (Fig. 34, O.C′), and ventrally are continued into well-pronounced **optic tracts** (Fig. 34), from which the **optic nerves** (Fig. 34, 2nd) arise. The two optic tracts cross each other in the middle line, where they become merged together, though the fibres do not intermingle, to form the **optic chiasma** (Fig. 34, O.C), so that the right eye is supplied with an optic nerve which arises entirely from the left side of the brain, and vice versa for the other eye. The **cerebellum** (**metencephalon**) (Fig. 37, CER) is a mere dorsal ridge of the anterior end of the **medulla oblongata** (**myelencephalon**) (Figs. 34 & 37, MED.OB).

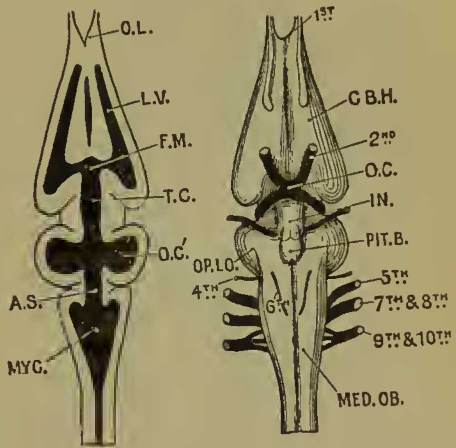


FIG. 34. Brain of Frog (*Rana*). The left-hand figure represents a dorsal dissection so as to show the relation and extent of the different cavities or ventricles; the right-hand one represents a ventral view of the brain. A.S = aqueduct of Syllvius (passage between the third and fourth ventricles); CB.H = cerebral hemisphere; F.M. = foramen of Monro; IN = infundibulum; L.V = lateral ventricles; MED.OB = medulla oblongata; MYC = myelocœle or fourth ventricle; O.C′ = optocœle (cavity of the optic lobes); OP.LO = optic lobes; O.C = optic chiasma; PIT.B = pituitary body; T.C = thalamocœle or third ventricle; 1st to 10th = first to tenth cranial nerves. The optic tracts are the black strands behind the optic chiasma.

The nerve commissures. In the frog, as in the dogfish and the rabbit, the two sides of the brain are connected to one another by certain tracts of nerve tissues or fibres known as commissures. The more important of these are the **anterior commissure**, passing from side to side of the posterior region of the cerebral hemispheres; the **median commissure**, passing from either side of the thalamencephalon; and the **posterior commissure**, connecting either side of the anterior part of the optic lobes. There are others which are only fully developed in mammals, and which are considered in the description of the rabbit's brain.

The **infundibulum** (Fig. 34, IN) and **hypophysis** (**pituitary body**, PIT. B) are well developed, but the saccus vasculosus of the dogfish is only represented by the merest vestige.

Rabbit. Alike in external form and internal organization, the brain of the rabbit, though comparatively simple, considered as a mammalian organ, presents a very great advance upon that of the frog. The gap that separates the two is, however, bridged by the structural features of the brain of reptiles and birds, and so much so, that the embryonic condition of the brains of all mammals is very similar to that of the Sauropsida [1].

The **cerebral hemispheres** (Fig. 35, CB.H) are relatively very large and have grown backwards over the optic lobes, and though in the rabbit there are no convolutions of their surfaces, as there are in the dog, they are clearly subdivided into **frontal** (F.L), **temporal** (T.L), and **parietal lobes** (P.L). In correlation with this division a marked differentiation of the lateral ventricle of each hemisphere into an **anterior**, a **posterior**, and an **inferior horn** (**cornu**) has arisen. The **olfactory lobes** (O.L) arise from the under surface of the hemispheres, and are continuous with the temporal lobes behind. The **thalamencephalon** (3rd V) is completely covered by the cerebral hemispheres, and its cavity or third ventricle (3rd V) is reduced to a mere median cleft; its sides are very much thickened to form the **optic thalami**, and upon the ventro-outer surface of these at their anterior ends is a rounded elevation, the **corpus geniculatum**. The floor of the infundibulum forms a rounded eminence called the **corpus mammillare** (Fig. 35, C.M), to which the pituitary body (PIT.B) is attached. The **mid-brain** (N & T) is relatively reduced in size; its ventricle, or **aqueduct of Syllvius** (A.S), is very narrow, and the **optic lobes** are almost solid, and are subdivided by a groove into an anterior **nates** (N) and a posterior **testes** (T). The **crura cerebri** (Fig. 35, C.C) are fibrous thickenings in the floor of the mid-brain, which extend from either hemisphere dorsal to the pons Varolii and corpus trapezoideum, along the length of the spinal cord. The **ventral pyramids** (V.P) are the continuation of the crura cerebri along the spinal cord. A little way behind the medulla oblongata they cross each other, or decussate.

The **cerebellum** is very large and has undergone differentiation into a middle portion, the **superior vermis** (S.V), and two **lateral**

[1] The Sauropsida is the class which includes reptiles and birds, just as the Icthyopsida is the class which includes fishes and Amphibia.

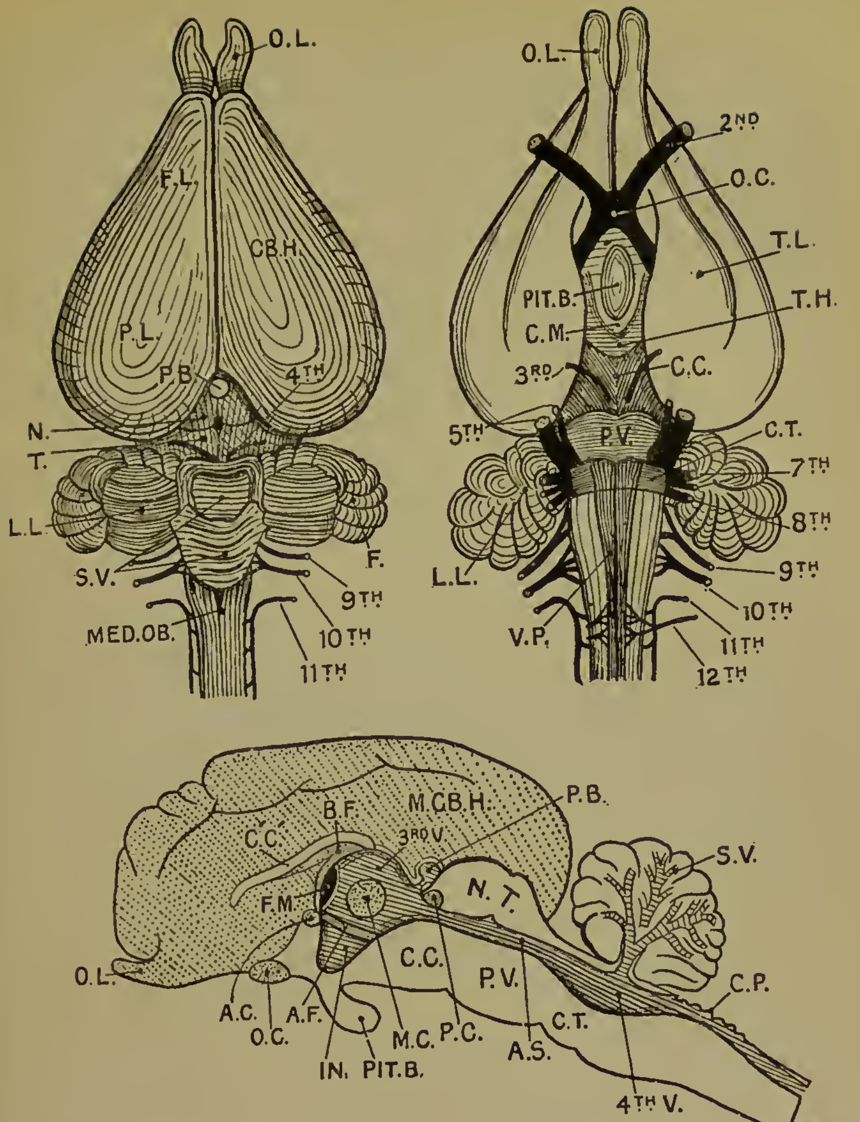


Fig. 35. Brain of the Rabbit (*Lepus*). The top left-hand figure represents a dorsal view, the top right-hand one a ventral view, and the lower figure a median vertical section passing between the two cerebral hemispheres. A.C = anterior commissure; A.S = aqueduct of Syllvius; A.F = anterior pillar of fornix; B.F = body of fornix; CB.H = cerebral hemispheres; C.C = crura cerebri; C′.C′ = corpus callosum; C.M = corpus mammillare (corpus albicans); C.T = corpus trapezoideum; C.P = choroid plexus; F.M = foramen of Monro; F = flocculi of cerebellum; F.L = frontal lobe of cerebrum; IN = infundibulum; L.L = lateral lobes of cerebellum; M.C = middle commissure; MED.OB = medulla oblongata; M.CB.H = mesial aspect of cerebral hemispheres; N = nates (anterior part of optic lobes); O.L = olfactory lobes; O.C = optic chiasma; P.C = posterior commissure; P.V = pons Varolii; P.B = pineal body; P.L = parietal lobe; PIT.B = pituitary body; S.V = superior vermis of cerebellum; T.H = thalamencephalon; T.L = temporal lobe of cerebrum; T = testis (posterior portion of optic lobes); V.P = ventral pyramids; 1st to 12th = first to twelfth cranial nerves; 3rd V = third ventricle; 4th V = fourth ventricle. The lower figure is a section through a sheep's brain.

lobes (L.L) with their **flocculi** (F); the lateral lobes are connected by two large ventral commissures, the **pons Varolii** (P.V) and the **corpus trapezoideum** (C.T). The cerebellum as a whole is connected with the medulla oblongata by dorsal tracts of fibres known as the **anterior, middle, and posterior peduncles** of the cerebellum. The wall of the cerebellum is not simple like that of the dogfish, but is much plicated; the result of this is a very great increase of nervous matter surface without a proportionate increase of size of the organ as a whole.

In addition to the anterior (Fig. 35, A.C), middle (M.C), and posterior commissures (P.C), which in the rabbit are more perfectly developed than in the dogfish or the frog—especially the middle commissure, which now forms a distinct structure apart from the base of the brain—there are present two others, the **corpus callosum** (Fig. 35, C′.C′) and the **fornix** (B.F & A.F). The former consists of a sheet of fibres in the roof of the lateral ventricles, and passes from one to the other, across the middle line; the latter consists of thin bands of fibres passing from one lateral (descending) cornu of the ventricle to that of the other, and is constituted by a median **body of the fornix** (Fig. 35, B.F) lying just in front of the third ventricle, and by **anterior** (Fig. 35, A.F) and **posterior pillars of the fornix**, which serve as the connecting channels between the two hemispheres.

The floor and sides of the anterior end of each lateral ventricle are markedly differentiated by the formation of two prominent thickenings or elevations, called the **corpus striatum** and **hippocampus major**.

The **pineal body** (Fig. 35, P.B) is displaced backwards and downwards by the backward growth of the cerebrum (cerebral hemispheres), and lies against the anterior part of the mid-brain, so that it no longer reaches to the roof of the skull. No trace of a parietal organ is found.

The two optic tracts do not simply contribute all their fibres to one optic nerve respectively, but divide at the optic chiasma into a larger and a smaller bundle, the larger one passing over to the other side and joining the smaller one of the other tract to form the optic nerve of that side; hence each optic nerve is contributed to by both tracts, but in major part by that of the opposite side.

Peripheral Nervous System.

This consists of two sets of nerves: **spinal** and **cranial**; the former set retain a more primitive arrangement than the latter. They form

the channels of communication between the outer surfaces of the body and the central nervous system, and in both cranial and spinal nerves two kinds of fibres may be distinguished, i. e. those which convey impulses from without to the central nervous system, the outcome of which is the production of sensation, and those which carry impulses in the reverse direction, from the central system outwards to the muscles, and the immediate manifestation of which is motion. The former are called **afferent or sensory fibres**, and the latter **efferent or motor fibres**.

SPINAL NERVES.

The spinal nerves of all Vertebrates arise from the spinal cord by two roots, one dorsal and the other ventral. These two roots differ in nature from each other, since the dorsal root contains only sensory fibres and the ventral root only motor fibres. Each dorsal root has a swelling or **ganglion** developed upon it, which consists principally of an aggregate of nerve-cells, with which the fibres of the root are connected. Ventrally to this ganglion the two roots unite to form a common trunk, the **spinal nerve**, which, therefore, consists of mixed fibres, i. e. sensory and motor.

Dogfish. In the dogfish the two roots do not arise in the same plane as they do in the frog and rabbit, but the dorsal ones take their origin in front of the ventral ones in such a way that the ventral roots of one side of the spinal cord alternate with those of the other, and lie opposite their corresponding dorsal ones. The dorsal ganglionated roots pass out from the spinal canal through the notches in the inter-vertebral plates (Fig. 1), while the corresponding ventral ones pass out from notches in the posterior margins of the vertebral plates.

Brachial plexus. In most fishes a certain number of the spinal nerves in the region of the pectoral fins are larger than those immediately in front or behind, and form a more or less complicated anastomosis, whence nerves pass outwards to the muscles of the fins. This anastomosis of spinal nerves for the supply of the anterior limbs of locomotion is called a **brachial plexus.** Among fishes it is of a very variable nature and cannot be reduced to a common plan, i. e. to one that would express equally well its fundamental characters for all fishes. In the dogfish it can hardly be said to exist at all; a certain number of spinal nerves pass outwards to the supply of the fins, but there is no well-defined anastomosis.

Lumbar or sciatic plexus. A similar plexus exists for the

supply of the posterior limbs of locomotion, which in the case of fishes are the pelvic fins. In the dogfish there is no well-defined lumbar plexus; a certain number of spinal nerves simply pass outwards to the pelvic fins without anastomosing.

Frog. In the frog there are ten pairs of spinal nerves, each arising by two roots, which unite to form the trunk of the nerve at their exit from the inter-vertebral foramina (Fig. 2).

The **first spinal** or **hypoglossal nerve** (Fig. 37, HYP) passes out between the first and second vertebræ and runs along the genio-hyoideus muscle to the root of the tongue (T), the muscles of which it supplies, and of which, therefore, it is the motor nerve. The dorsal root is exceedingly slender, and this is interesting, since in mammalia the hypoglossal has become the last cranial nerve; and it is known that during the development of the sheep this nerve (twelfth cranial) arises by two roots, the dorsal of which subsequently disappears. So it would appear that in the frog we have the first indication of that retrogression of the dorsal root that has almost reached its final stage in the mammalia.

The **second** and **third spinal nerves** pass out between the second and third and third and fourth vertebræ respectively, and subsequently unite to form the **brachial plexus**. There is a slight variation with regard to the behaviour of the third nerve, which sometimes becomes completely merged with the second; at other times it merely lies in contact with it, or may send off a small twig to it. The second nerve is known as the **brachial nerve**, and, together with some fibres derived from the third nerve, supplies the muscles of the arm.

The **fourth, fifth,** and **sixth spinal nerves** pass out through their corresponding inter-vertebral foramina and supply the muscles of the body-wall; their distribution, like their origin, is segmental.

The **seventh, eighth, ninth,** and **tenth spinal nerves** pass out through their respective inter-vertebral foramina; the ninth between the sacral vertebra and the urostyle (Fig. 9), and the tenth through the coccygeal canal in the latter. They all subsequently unite to form the **sciatic plexus**, from which the **sciatic** and **coccygeal** nerves arise, the latter being the continuation of the tenth nerve after it has supplied the sciatic plexus. The mode of formation of the plexus is subject to considerable variation.

The nerves which pass out between the vertebræ in front of the sacral vertebra are called presacral, and those which pass out behind post-sacral.

Rabbit. In correspondence with the division of the vertebral column into cervical, thoracic, lumbar, sacral, and caudal regions, the nerves emerging from these regions are named accordingly (Fig. 38, 1st C–8th C, 1st T–12th T, 1st L–7th L, 1st S–4th S).

There is, however, a certain amount of ambiguity in counting the spinal nerves, since in the cervical region they are numbered from the vertebræ in *front* of which they arise, while in the thoracic and other regions they are named from the vertebræ *behind* which they arise. It follows from this that there is one cervical nerve more than corresponding vertebræ, since the first arises in front of the atlas, between it and the occipital condyles, and the last or eighth behind the last cervical and in front of the first thoracic vertebra.

The third cervical spinal nerve (Fig. 38), in addition to supplying the region of the neck in which it arises, gives off a large branch, the **great auricular** (G.A), to the ear.

Brachial plexus. This is formed by the union of the fifth to eighth cervical and of the first thoracic nerves, and supplies the muscles and skin of the arms and shoulders. There are four chief nerves derived from it, i. e. the **ulnar**, **median**, **musculo-spiral**, and **subscapular**. The ulnar and median nerves supply the flexor muscles of the arm, and the musculo-spiral the extensor muscles. The subscapular supplies some of the muscles of the shoulder-blade.

The lumbo-sacral plexus. This is formed by the union of the fifth to seventh lumbar and of the first to third sacral nerves, though not infrequently a backward shifting takes place, so that the plexus arises from between the sixth lumbar and fourth sacral. From it there arise three principal nerves: the **sciatic nerve**, the largest of the three, supplying the flexor muscles of the leg; the **crural nerve**, supplying the extensor muscles of the leg; and the **obturator nerve**, passing out through the obturator foramen to the muscles of the thigh.

The remaining cervical, thoracic, and lumbar nerves supply the body muscles in the regions in which they run.

The **phrenic nerve** (Fig. 38, P) is the motor nerve of respiration. It arises from the fourth, fifth, and sixth cervical spinal nerves, and passes through the thoracic cavity behind the heart to the muscles of the diaphragm (Fig. 38, lower D). Not infrequently it arises from the fourth and sixth nerves only.

Sympathetic System.

This consists of two ganglionated chains (Fig. 38) running along the length of the body on either side of the vertebral column, and is concerned with the innervation of the alimentary canal, the vascular system, and the glandular organs of the body. It is primitively uniformly segmented, and it retains its segmentation more or less completely throughout life, but in some portions of the body, such as the neck, its metameric character becomes lost or profoundly modified. Each ganglion (Fig. 38, SG) is connected with the cerebro-spinal system by means of small branches called **rami communicantes** (R.C), which leave the spinal nerves soon after their exit from the inter-vertebral foramina. In the thoracic, lumbar, and sacral regions (Fig. 38) the sympathetic ganglia correspond in number to the spinal nerves, but in the cervical region they are much reduced.

In the frog the sympathetic is connected with the cranial nerves by virtue of a connexion with the Gasserian ganglion of the trigeminal nerve and the ganglion of the vagus.

In the rabbit the cervical ganglia are reduced to three (Fig. 38, C.S), an anterior one a little in front of the larynx, a median one (Fig. 38, M.C) just anterior to the subclavian artery, and a posterior (Fig. 38, I.C) just behind the artery, and more or less merged with the first thoracic ganglion (1st T). As it passes the subclavian artery the sympathetic chain forms a ring through which the artery runs, and which is known as the **annulus of Vieussens** (Fig. 38). The sympathetic chain is connected at its anterior termination with the maxillary and mandibular branches of the trigeminal nerve; with the former by means of the **spheno-palatine ganglion**, and with the latter by means of the **otic** and **submaxillary ganglia**.

In the mesentery supporting the alimentary canal of the rabbit there are developed three ganglionated masses in connexion with the sympathetic nervous system (Fig. 38). The first of these, the **cœliac ganglion** (C.G), lies between the cœliac (C) and anterior mesenteric arteries (A.M.A), rather nearer the latter than the former; while the second one, the anterior **mesenteric ganglion** (A.M), lies on either side of the artery from which it derives its name. The third ganglion is situated just behind the posterior mesenteric artery (P.M.A) and receives its name from that. All three ganglia are connected together by nerve fibres, and from them nerves pass out and run in company with the arteries of the same name, the muscular walls of which, as

well as the muscular walls of the alimentary canal which they supply, are innervated by them. The anterior mesenteric ganglion is connected with the sympathetic chain by means of the **greater** and **lesser splanchnic nerves** (G.S & L.S), the former of which arises from the chain at the ninth and tenth thoracic ganglia, and the latter at the eleventh and twelfth. As often as not, however, the splanchnic nerves, instead of passing to the anterior mesenteric, pass to the cœliac ganglion instead.

These three ganglia may be regarded as peripheral outgrowths of the sympathetic nervous system. They are connected with the cerebro-spinal system by a branch of the vagus nerve (Fig. 38, V) which passes to the cœliac ganglion.

In the dogfish there is a large anterior ganglion near the anterior cardinal sinus, and the more posterior ganglia are closely connected with the medullary portion of the supra-renal bodies. The study of development shows that the sympathetic ganglia are but enlargements of the spinal nerves in which nerve-cells are aggregated. In an early period of their development these primitive enlargements separate into two portions, one of which becomes the ganglion of the adult, and the other the medullary portion of the glandular supra-renal bodies. The condition found in the dogfish is very similar to this embryonic condition, while in the frog and rabbit the ganglia are only connected with the glands by nerve fibres, and are themselves removed from them, and become ranged in two rows along the length of the body on either side of the dorsal aorta.

Cranial Nerves.

In certain features of their development the cranial nerves resemble those of the spinal cord, and among the lower Vertebrata transitional stages between the two sets of nerves may be traced. The fact that in the adult they arise by a single root instead of a double one, as do the spinal nerves, is not of much importance, since we have already seen that, in the case of the frog, one of these roots belonging to the first spinal nerve is much reduced, while in many mammals—man included—it may be reduced or altogether wanting; so that their first spinal nerve (which is not homologous with the first spinal of the frog, ante, pp. 128) arises, like the cranial nerves, by a single root. Moreover, in the embryos of certain mammals the last cranial nerve, i.e. the hypoglossal, primitively arises by a double root, like an

ordinary spinal nerve, but the dorsal one disappears before extra-uterine life commences. In addition, the third, sixth, twelfth, and perhaps the fourth cranial nerves, arise from the brain in the same way that the ventral roots of the spinal nerves arise from the spinal cord, i.e. as direct outgrowths of its ventral surface. The eighth, ninth, and tenth, and in part the fifth and seventh, arise not in direct connexion with the brain, but with their ganglia, which are localized thickenings of the epiblast, and only later become connected with it; this is a mode of development which simulates that of the dorsal roots of the spinal nerves.

Although the cranial and spinal nerves thus resemble each other, they differ in other respects, for, with the exception of the olfactory (*first*), the optic (*second*), and the auditory (*eighth*), the roots of all the cranial nerves contain mixed fibres, i.e. both sensory and motor, and those which primitively arise dorsally subsequently shift to the ventral surface. The fourth nerve is an apparent exception, since it leaves the dorsal surface of the brain; but in reality it arises from the ventral portion of the brain and passes upwards through its substance to the dorsal surface, whence it emerges to the exterior.

The cranial nerves are paired and numbered from before backwards. In the dogfish and frog there are ten, and in the rabbit twelve.

Dogfish. The **first** or **olfactory nerve** arises as two large bundles from the front of the olfactory lobes (Fig. 36, OL.L) and passes direct to the folds of the olfactory epithelium (OL.EP); they contain sensory fibres only.

Second or **optic nerve** passes from the optic chiasma, formed by the decussation of the optic tracts, through the optic foramen to the eyeball, whence its fibres spread out over the inner surface of the retina; it contains only sensory fibres.

Third or **oculomotor nerve** (Fig. 36, 3rd) is a very slender one, arising from the ventral surface of the mid-brain beneath the optic lobes, and supplying all the eye-muscles except the external rectus and the superior oblique; it is thus wholly motor: it is secondarily connected with the ciliary ganglion, derived from the sympathetic.

Fourth or **pathetic** or **trochlear nerve** arises apparently from the dorsal surface of the brain (Fig. 36, 4th), between the optic lobes and the cerebellum, whence it passes out to supply the superior oblique eyeball muscle. It contains sensory as well as motor fibres, and these supply the connective tissue of the eye.

Fifth or **trigeminal nerve** arises from the side of the medulla

oblongata by two roots, a large lateral sensory and a small ventral motor one, very close to the seventh and eighth, and passes out with the former through the foramen in the hinder part of the orbit (Fig. 36). The sensory root bears a large ganglion, the **Gasserian ganglion.** It divides into two main branches, i.e. the **ophthalmic branch** (Fig. 36, OPH.D of 5th), that supplies the mucous canals (sensory tubes) of the dorsal surface of the snout and forehead; the **maxillo-mandibular**, which in its turn divides into the **maxillary branch** (Fig. 36, MAX.D of 5th), supplying the mucous canals of the upper jaw, snout, and upper lips, and also teeth of upper jaw and roof of mouth, and the **mandibular branch** (Fig. 36, MAN.D of 5th), which is a mixed nerve supplying the muscles of the lower jaw and integument of lower lip.

Sixth or abducens nerve arises in the middle line from the ventral surface of the medulla, and passes out with the fifth and seventh to supply the external rectus muscle of the eyeball.

Seventh or facial nerve contains mixed fibres, and arises from the medulla oblongata very close behind the fifth; it leaves the skull in company with it and through the same foramen. It possesses two distinct ganglia, one in connexion with its sensory and the other with its mixed branch. It divides into three main branches, i.e. the **ophthalmic branch** (Fig. 36, OPH.D of 7th), which, like the corresponding branch of the fifth, is a sensory nerve; it leaves the skull through a separate foramen (Fig. 17, FOR.OPH 7th), travelling in company with that across the orbit to its distribution; just previous to leaving the orbit of the eye, the ophthalmic branches of the fifth and seventh nerves unite and reach the snout as a single trunk, which breaks up into a number of fibrils distributed to the sensory tubes; the **palatine branch** (PA.D 7th) is a slender sensory nerve supplying the roof of the mouth and upper jaw, and anastomosing with the maxillary division of the fifth; the **hyo-mandibular** is the largest and most posterior of the three, and though a mixed nerve is mainly motor; it principally supplies the muscles of the hyoidean and mandibular arches; it divides into three branches: a sensory **internal mandibular** or **chorda tympani** (Fig. 36, CH.T), a sensory **external mandibular** (EX.MAN), and a main branch (M.HY), wholly motor. A small branch of the seventh nerve, the **buccal branch** (BU.D of 7th), travels in company with the maxillo-mandibular division of the fifth; in the figure it has been represented as being pulled outwards from underneath that.

Eighth or auditory nerve (Fig. 36, 8th) is a very short nerve, arising from the medulla just behind the seventh, and immediately

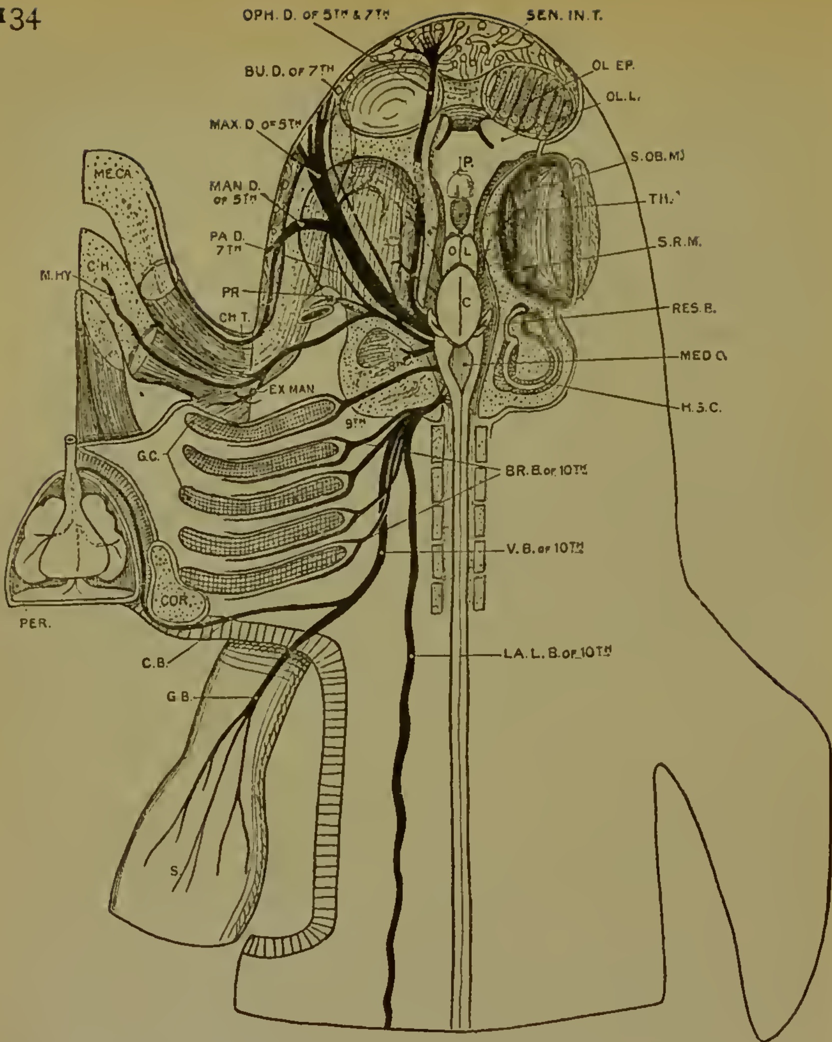


FIG. 36. Dorso-ventral dissection of Dogfish (*Scyllium*), to show brain, spinal cord, and cranial nerves. The buccal cavity has been cut open along the middle line, the plane of incision passing to one side of the pericardium and traversing the shoulder-girdle; the floor of the buccal cavity, the pericardium, shoulder-girdle, and stomach were then turned towards the left so as to lie in one plane with the animal's body, and the dissection proceeded with. BU.D of 7th = buccal branch of seventh nerve; it properly lies underneath MAX.D of 5th, but has been pulled forwards for the sake of clearness; BR.B of 10th = branchial branches of vagus; C = cerebellum; C.B = cardiac branch of vagus nerve; COR = coracoid cartilage cut across; CH.T = chorda tympani nerve; C-H = cerato-hyal cartilage; EX.MAN = external mandibular branch of seventh; G.B = gastric branch of vagus; G.C = gill-clefts; H.S.C = horizontal semicircular canal of internal ear; LA.L.B of 10th = lateral line branch of vagus nerve; MED.O = medulla oblongata; MAX.D of 5th = maxillary division of trigeminal nerve; MAN.D of 5th = mandibular division of trigeminal; M.HY = main branch of hyo-mandibular division of facial nerve; ME.CA = Meckel's cartilage (lower jaw); OL.EP = olfactory epithelium; OL.L = olfactory lobe of brain; O.L = optic lobes of brain; OPH.D of 5th & 7th, ophthalmic division of the fifth & seventh nerves; P = prosencephalon; PA.D 7th = palatine branch of facial nerve; PER = pericardium; PR = prespiracular branch of seventh; the oval cavity represented just behind it is the spiracle; RES.B = restiform body; S = stomach; S.OB.M = superior oblique muscle of eyeball; S.R.M = superior rectus muscle of eyeball; SEN.IN.T = sensory integumentary tubes; TH = thalamencephalon; V.B of 10th = visceral branch of vagus; 1st to 10th = first to tenth cranial nerves.

piercing the internal wall of the auditory capsule supplies the internal ear. It is wholly sensory.

Ninth or glosso-pharyngeal nerve (Fig. 36, 9th) is a mixed nerve, and arises from the ventro-lateral surface of the medulla oblongata, not far behind the auditory nerve; outside the skull it passes across the floor of the auditory capsules and divides into an anterior **hyoidean branch** which supplies the posterior border of the hyoid arch, and a posterior **branchial branch** which supplies the anterior border of the first branchial arch. The two branches of the nerve thus form a fork, one prong of which lies anterior to the first gill-cleft (G.C.), and the other, larger one, posterior to it. The facial nerve has similar relations to the spiracle, which is a vestigial gill-cleft, its palatine branch corresponding to the anterior prong of the glosso-pharyngeal, and its hyo-mandibular to the posterior prong.

Tenth or vagus or pneumogastric nerve (Fig. 36, 10th) is a large nerve arising by several small roots from the side of the hinder part of the medulla; it leaves the skull through a foramen to the outer side of the condyle. It then runs along the dorsal wall of the anterior cardinal sinus and gives off in succession four **branchial nerves** (BR.B of 10th), which supply the second to fifth branchial clefts (G.C), each nerve dividing into a smaller anterior and a larger posterior branch. The main trunk is continued backwards as the **visceral branch** (V.B of 10th), which divides into the **cardiac nerve** (C.B), supplying the heart, and the **gastric nerve** (G.B) going to the stomach (S). The **lateral line nerve** (LA.L.B of 10th) arises from the vagus soon after its origin, and runs back as a large nerve parallel to the lateral line vein; in the dogfish it lies deeply situated between the peritoneum and body-wall, but in some other fishes it lies just beneath the skin.

The Frog and **Rabbit. First or olfactory nerve.** This is a very short nerve, and breaks up into very numerous filaments that supply the olfactory epithelium. In the frog the nerve leaves the skull by the sphenethmoid canal before dividing, and in the rabbit the filaments pass through the perforated cribriform plate.

Second or optic nerve. In the frog *all* the fibres of the optic tract of one side pass over at the optic chiasma to form the optic nerve of the other, but in the rabbit only the major portion of the fibres of the optic tract of one side pass over to form the optic nerve of the opposite side, the remainder of it being composed of fibres derived from the optic tract of the same side. As in the dogfish, the optic nerve is wholly sensory and supplies the retina of the eye.

Third or oculomotor. In the frog (Fig. 37, 3rd) this nerve leaves the skull just in front of the fifth, and in the rabbit it leaves the skull

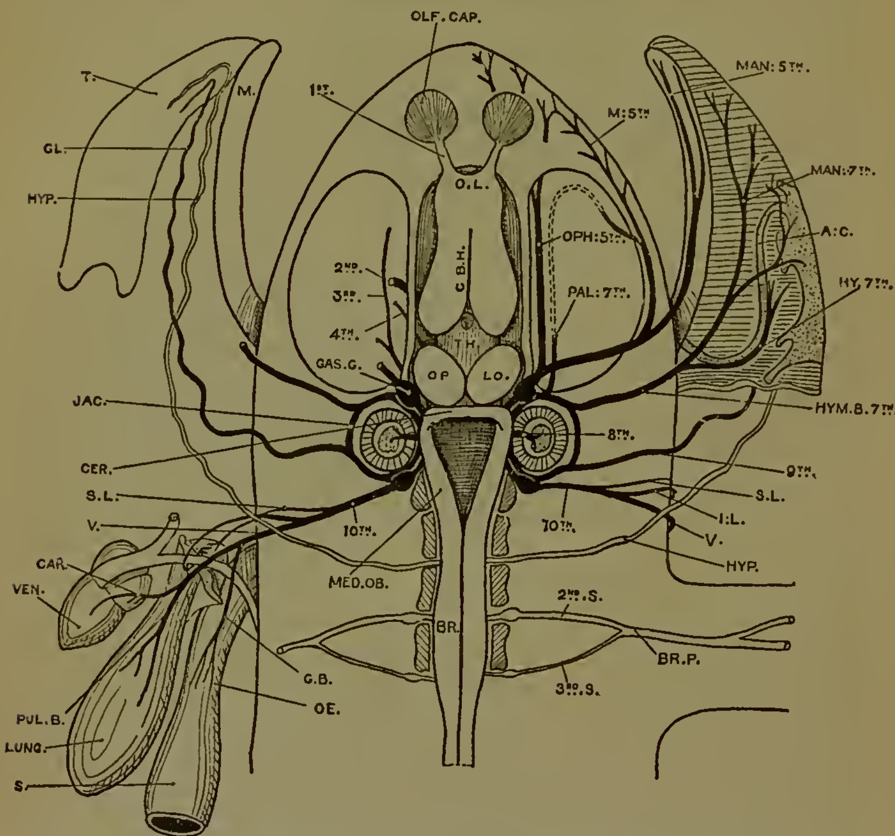


FIG. 37. Dorso-ventral dissection of Frog (*Rana*), to show brain, cranial nerves, and part of spinal cord and nerves. The dissection is similar to that represented in Fig. 36. A.C = anterior cornu of hyoid plate; BR.P = brachial plexus; BR = brachial enlargement of spinal cord; CB.H = cerebral hemispheres; CER = cerebellum; CAR = cardiac branch of vagus nerve; G.B = gastric branch of vagus; GAS.G = Gasserian ganglion; GL = glosso-pharyngeal nerve; HY 7th = hyoidean branch of hyo-mandibular; HYM.B 7th = hyo-mandibular branch of facial nerve; HYP = hypoglossal nerve; I.L = posterior laryngeal nerve; JAC = anastomosis of Jacobson (union of seventh and ninth nerves); M = mandible of lower jaw; M 5th = maxillary division of fifth nerve; MAN 5th & MAN 7th = mandibular branch of trigeminal and facial nerves respectively; MED.OB = medulla oblongata; OE = œsophagus; O.L = olfactory lobes; OLF.CAP = olfactory capsules; OP.LO = optic lobes; OPH 5th = ophthalmic division of trigeminal; PAL 7th = palatine branch of the facial; PUL.B = pulmonary branch of vagus; S = stomach; S.L = anterior laryngeal nerve; T = tongue; TH = thalamencephalon; V = vagus; VEN = ventricle of heart; 1st to 10th = first to tenth cranial nerves; 2nd S & 3rd S = second and third spinal nerves.

in company with the fourth and sixth, through the sphenoidal fissure[1]. It supplies the same muscles as that in the dogfish.

[1] The sphenoidal fissure of the rabbit's skull represents the foramen lacerum anterius and the foramen rotundum of the dog's.

Fourth or **pathetic nerve.** As in the dogfish, except that in the rabbit it contains no sensory fibres.

Fifth or **trigeminal nerve** in the frog (Fig. 37, 5th) bears a large ganglion, the Gasserian ganglion (Fig. 37, GAS.G), soon after its origin and before it leaves the skull. It pierces the cranial wall just in front of the auditory capsule, and immediately divides into two branches, of which the posterior one again divides. The anterior of these branches is the **ophthalmic nerve** (OPH 5th), which in part supplies the olfactory epithelium and in part the skin of the snout, forehead, and eyelids; from it there arises a large nerve, the **palatine nerve**, which unites with the **palatine branch** of the seventh nerve, and supplies the mucous membrane of the palate, the Harderian gland, and the inner surface of the maxilla; it follows a very complicated course, and forms a large number of inosculations with terminal twigs of branches of the trigeminal. The posterior branch divides into two, the **mandibular** (MAN 5th) and **maxillary** (M 5th) **branches** of the fifth, the former of which supplies the muscles and skin of the lower jaw, and the latter the roof of the mouth, skin of the upper jaw, snout, and the Harderian glands; in addition it forms an inosculation with the palatine nerve (PAL 7th), shown in the figure by dotted lines.

In the rabbit (Fig. 38, O) the **ophthalmic division** passes out with the third, fourth, and sixth cranial nerves, through the sphenoidal fissure, and through the foramen lacerum anterius in the dog's skull, and supplies the skin of the forehead, snout, and eyelids, and the lachrymal glands; it is entirely sensory. The second division, or **maxillary branch** (MX), passes out through the foramen rotundum in the dog's skull, and becomes connected with the spheno-palatine ganglion of the sympathetic, and supplies the lachrymal and Harderian glands, the palate, and the teeth of the upper jaw; thence passing through the infra-orbital canal it reaches the skin of the upper jaw, snout, and upper lips, which it innervates; it is an entirely sensory nerve. The third division, or **mandibular branch** (Fig. 38, MN), is a mixed nerve, being composed of both motor and sensory fibres; from it is derived the great sensory nerve of the tongue, the **lingual** or **gustatory nerve** (Fig. 38, L), and several other branches which supply the teeth of the lower jaw, the integument of the lower jaw and lip, and the masticatory, and a few of the hyoid muscles. The sensory portion of this branch is connected with the sympathetic nervous system by means of the submaxillary and otic ganglia. In the dog's skull it passes out through the foramen ovale.

Sixth or **abducens nerve.** Essentially the same as that in the dogfish.

Seventh or **facial nerve** passes out in the rabbit from the internal auditory meatus and the stylo-mastoid foramen, and in the frog it first unites with the Gasserian ganglion of the fifth nerve, and leaves the skull in company with the mandibulo-maxillary branch of that (Fig. 18). In the frog (Fig. 37, 7th) it divides into a **palatine branch** (PAL 7th), which ultimately anastomoses with a branch of the trigeminal; a **chorda tympani** branch, which pierces the tympanum; a **hyo-mandibular branch** (HYM.B 7th), which unites with the anterior ramus (JAC) of the glosso-pharyngeal (anastomosis of Jacobson) to form a single trunk that passes down the posterior wall of the Eustachian tube to the angle of the jaw; and then divides into a **mandibular branch** (MAN 7th), which passes forward along the mandible and supplies small twigs to the mucous membrane of the mouth, and into a **hyoidean branch** (HY 7th) that passes along the anterior cornu of the hyoid bone. In the rabbit the **palatine branch** (Fig. 38, PL) leaves the cranium by the internal auditory meatus, thence passes across the orbit to reach the epithelium of the palatine region of the buccal cavity; the **chorda tympani (internal mandibular) branch** passes through the tympanic cavity (middle ear), and supplies the submaxillary and sub-lingual glands, and the blood-vessels connected with them. The **main branch** (Fig. 38, VII) leaves the cranium by the stylo-mastoid foramen, thence passes over the masseter muscle to the region of the snout, where it divides into numerous branches that supply the muscles of the face; it is entirely motor.

In the rabbit and frog only one of the two ganglia present in the dogfish, i.e. the **geniculate ganglion**, is present at the origin of the nerve, the other having become incorporated with the Gasserian ganglion of the trigeminal nerve; and the nerves that arose from the lost ganglion, i.e. ophthalmic division of the 7th, buccal, and external mandibular, have also disappeared.

Eighth or **auditory nerve** arises from the side of the medulla oblongata, close to the facial nerve (Figs. 34 & 35), and passes direct to the ear, where it divides into cochlear and vestibular branches. In the frog (Fig. 34) it arises in common with the seventh nerve, but almost immediately separates from it.

Ninth or **glosso-pharyngeal** is a mixed nerve, and in the frog (Fig. 34) arises in common with the tenth, from which it soon separates, and leaves the skull immediately behind the auditory

capsule (Fig. 37), when it divides into an anterior branch (JAC) (anastomosis of Jacobson, see seventh nerve), which unites with the seventh nerve, and a posterior much larger branch (GL), which runs forward to the floor of the mouth, whence it crosses to the inner side of the hypoglossal nerve (HYP), and following a sinuous course supplies some of the hyoid muscles and the mucous membrane of the pharynx. In the rabbit (Fig. 38, G) it leaves the skull with the vagus and spinal accessory nerves through the foramen lacerum posterius, and immediately turns forwards to enter the substance of the tongue; its fibres are distributed both to the muscles of that and to the epithelium, so that this branch is sensory as well as motor. It also gives off branches to the pharyngeal wall.

In the dogfish the glosso-pharyngeal nerve supplies the first gill-cleft, and in small part the pharynx also, by a small pharyngeal branch; but in terrestrial Vertebrates there are no gill-clefts in adult life, and consequently that portion of the nerve which supplies the first of them has disappeared, and the pharyngeal branch has acquired greater development and become its principal part. But the tadpole of the frog is essentially a fish, and it is interesting to know that during its tadpole stage the glosso-pharyngeal nerve is like that of the dogfish, in that it forks round the first gill-cleft and gives off a small pharyngeal branch to the pharynx. At the time of the metamorphosis, when lungs develop and the gill-clefts disappear, the part which supplied the first gill-cleft retrogresses, and that branch which supplied the pharynx grows forwards to the tongue and becomes the main branch of the nerve. Hence, in the course of the ontogeny of the frog, we can trace the changes by which the primitively respiratory ninth nerve became converted into a mainly gustatory sensory nerve; it still retains in these higher forms, however, some of its original characters, inasmuch as in them it supplies some of the muscles of the tongue and pharynx which contribute in some degree to the movements of respiration.

Tenth or vagus nerve leaves the skull in the frog by the vagus canal (Fig. 18, 10th FOR), an opening in the exoccipital bone, and supplies branches to the heart (Fig. 37, 10th & CAR), lungs (PUL.B), larynx (S.L & I.L), stomach (G.B), pharynx, a few of the hyoid muscles, and the skin of the scapular region. In the rabbit it leaves the skull by the foramen lacerum posterius (Fig. 20), and passes backwards close to and parallel with the carotid artery (Fig. 38, V) to the thorax, whence it reaches the œsophagus, along which it travels to the stomach,

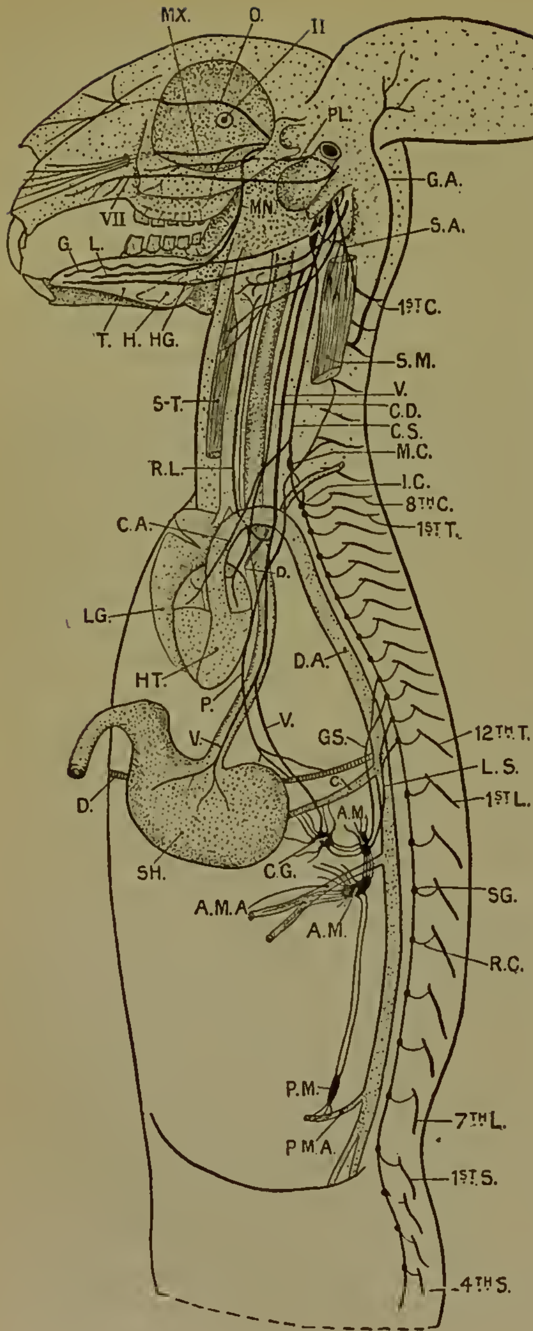


FIG. 38. Cranial and spinal nerves and the sympathetic nervous system of Rabbit (*Lepus*). A side dissection, semi-diagrammatically represented. A.M = anterior mesenteric ganglion of sympathetic; A.M.A = anterior mesenteric artery; C = cœliac artery; C.A = cardiac accelerator nerve; C.D = cardiac depressor nerve; C.G = cœliac ganglion of sympathetic; C.S = cervical portion of sympathetic nerve-chain; 1st & 8th C = first and eighth cervical spinal nerve; D (upper one) = ductus arteriosus; it joins the aortic and pulmonary arches, but the latter is not represented; the ductus would join it just where the index line points; D (lower one) = diaphragm; D.A = dorsal aorta; G = glosso-pharyngeal; G.A = great auricular nerve; GS = greater splanchnic nerve; H = hyoid bone; HG = hypoglossal nerve; HT = heart; I.C = posterior cervical ganglion of sympathetic; L = lingual branch of mandibular nerve; L.G = right lung; L.S = lesser splanchnic nerve; 1st & 7th L = first and seventh lumbar spinal nerve; M.C = middle cervical ganglion; MX = maxillary division of trigeminal; MN = mandibular division of trigeminal; O = ophthalmic branch of trigeminal; P = phrenic nerve; PL = palatine division of facial nerve; P.M = posterior mesenteric ganglion of sympathetic; P.M.A = posterior mesenteric artery; R.C = rami communicantes; R.L = recurrent (posterior) laryngeal nerve; S.A = spinal accessory nerve; S.M = stylo-mastoid muscle; SH = stomach; S-T = sterno-thyroid muscle; SG = sympathetic ganglia; 1st & 4th S = first and fourth sacral spinal nerves; T = tongue; V = vagus; 1st & 12th T = first and twelfth thoracic spinal nerves; II & VII = second and seventh cranial nerves. The trachea lies just behind the sterno-thyroid muscle (S-T) and its top dilated part represents the larynx. The dotted tube behind it is the œsophagus.

the walls of which it supplies. It bears a ganglionic enlargement immediately outside the skull, and a little way behind this gives off a small branch, the **anterior laryngeal nerve**, to the larynx and crico-thyroid muscle. At the anterior portion of the thorax there is given off a branch which on the right side loops round the subclavian artery, but on the left round the ductus arteriosus, and thence round the aortic arch (Fig. 38) ; on either side each runs forward along the trachea to reach the larynx; this branch is the **recurrent laryngeal nerve** (Fig. 38, R.L) Its origin, at a great distance from the part which it innervates, is due to the long neck which, as it developed, carried the heart and the roots of the great vessels back from their primitive position in the throat ; and since this nerve passes towards the larynx posteriorly to the roots of the great blood-vessels, it is carried back with them in the form of a gradually elongating loop. If the student will refer to Fig. 37 he will see that the vagus gives off two branches to the larynx, in the frog as in the rabbit; there is an anterior laryngeal (S.L) which passes directly to the larynx, and a posterior laryngeal (I.L) which passes round the aortic arch before reaching the larynx. Now if the frog were to develop a long neck the larynx would have to remain in its original position, but the heart and great blood-vessels would be carried backwards as the neck elongated, and with them the posterior laryngeal nerve: hence the condition which it exhibits in the rabbit would be attained. The anterior laryngeal nerve gives origin to a very delicate nerve which runs along the trachea parallel to the cervical sympathetic nerve to the auricles of the heart in the wall of which it ends ; this nerve is known as the **cardiac depressor nerve** (Fig. 38, C.D), since stimulation of its peripheral end slows, and, if the stimulus be sufficiently strong, may completely suspend the action of the heart. While the vagus passes through the thorax it gives off delicate fibres to the heart and lungs, which are known respectively as the **cardiac** and **pulmonary plexuses**.

If the student will now compare the vagus nerve in the dogfish, frog, and rabbit, by means of Figs. 36, 37, & 38, he will see at once that the nerve in the two terrestrial animals (frog and rabbit) differs from that in the aquatic one (dogfish), in that in them only the visceral branch (Fig. 36, V.B of 10th) of the dogfish is represented. Obviously animals, which do not possess gill-clefts, do not need branchial branches to the nerve ; and, with respect to the lateral line branch, terrestrial Vertebrates do not possess sensory (mucous) tubes like those which this branch supplies in the integument of fishes. But, as in the

case of the glosso-pharyngeal, so in that of the vagus, the tadpole of the frog in respect of this nerve as in other characters is a veritable fish; for in it the vagus nerve possesses three branchial branches which supply the posterior three gill-clefts (the first one being supplied by the glosso-pharyngeal), and a lateral line branch which extends the length of the body just beneath the skin. At the time of the metamorphosis, when the tadpole becomes the frog, and the gill-clefts and tail atrophy, and the lungs become functionally active, the branchial and lateral line branches of the nerve undergo retrogression, only the visceral branch persisting. Thus the frog in its ontogeny fills the gap in respect of these nerves, as in respect of other characters also, between the aquatic Vertebrates and the terrestrial ones which have arisen from the same primitive stock as them; the terrestrial forms in the course of their evolution have lost some of their primitive characters, but fishes still permanently retain them, while some amphibians retain them only in the earlier phases of their development.

The next two cranial nerves, i. e. the eleventh or **spinal accessory**, and the twelfth or **hypoglossal**, are not present as such, in the dogfish or the frog; in the latter animal the hypoglossal is the first spinal nerve, but the other is not apparently represented. In fishes we may find all stages in the confluence of the first two vertebræ with the skull, and in some mammals (sheep, &c.) the hypoglossal arises like the spinal nerves by two roots, one of which subsequently disappears, so that it is very probable that the hypoglossal and spinal accessory nerves of the rabbit are spinal nerves, which have become cranial ones by confluence of the anterior two vertebræ with the occiput of the skull.

The **spinal accessory nerve** (Fig. 38, S.A) arises from the side of the medulla oblongata just behind the vagus by several roots, the most posterior of which is situated some way back; it leaves the skull (Fig. 38, S.A) in company with the glosso-pharyngeal and vagus nerves through the foramen lacerum posterius and supplies the stylo-mastoid muscle (Fig. 38, S.M).

The **hypoglossal nerve** (Fig. 38, HG) arises from the ventral surface of the medulla, immediately to the outer side of the ventral pyramids, by a number of roots, very similar to the ventral roots of a spinal nerve. It leaves the skull in two divisions on either side through two small openings in the occipital condyles, the **condylar foramina**. The main branch passes forward to the tongue (Fig. 38, HG), the muscles of which it supplies. The smaller branch, derived from the main one, passes backwards and supplies the sterno-thyroid

muscle (Fig. 38, S-T); this branch is called the **ramus descendens**, and may be easily confounded in the course of a dissection with the anterior laryngeal, but from this it may be distinguished, apart from its origin and distribution, by the fact that it passes externally to the carotid, while the laryngeal nerve passes internally.

TABULATION OF THE MORE IMPORTANT CHARACTERS OF THE NERVOUS SYSTEM.

	Dogfish.	Frog.	Rabbit.
Brain.	Prosencephalon simple.	Prosencephalon has grown forwards and formed two cerebral hemispheres.	As in the frog, but each hemisphere is marked into three regions, i.e. frontal, parietal, and temporal lobes. The cerebrum has grown backwards over the thalamencephalon and optic lobes.
	Olfactory lobes very largely developed.	Olfactory lobes not largely developed.	Olfactory lobes not disproportionally large.
	The two sides of the brain are connected by an anterior, middle, and posterior commissure.	As in dogfish.	In addition to the three commissures, there are two others, a corpus callosum and a fornix, which connect the two sides of the cerebrum.
	Optic lobes not divided (corpora bigemina).	Optic lobes as in dogfish.	Optic lobes divided into nates and testes (corpora quadrigemina).
	Cerebellum very large and simple.	Cerebellum rudimentary.	Cerebellum very large and complex; its wall plicated.
	The primitive cranial flexure disappears.	The primitive cranial flexure disappears.	In addition to the primitive flexure (parietal bend) two others appear in the course of development, i.e. the cervical and Varolian flexures.

	Dogfish.	Frog.	Rabbit.
Cranial nerves. Optic. II.	All the fibres of the optic tract at the optic chiasma cross to the other side. The optic nerve is a sensory one.	All the fibres of the optic tract at the optic chiasma cross to the other side. Sensory.	Only the major portion of the fibres of the optic tract of one side cross to the other side at the optic chiasma; the minor portion contribute to the optic nerve of the same side. Sensory.
Trigeminal. V.	The maxillary and mandibular branches of the trigeminal arise from a common branch, the maxillo-mandibular.	The maxillary and mandibular branches as in dogfish.	The maxillary and mandibular branches arise separately, and the latter gives origin to the lingual nerve, the principal sensory nerve of the tongue.
	The ophthalmic and maxillary divisions are wholly sensory; the mandibular is a mixed nerve.	The ophthalmic and maxillary are sensory nerves and the mandibular a mixed one.	The ophthalmic and maxillary are sensory and the mandibular a mixed one.
Facial. VII.	The facial nerve arises in connexion with two ganglia.	One of the ganglia of the facial nerve has merged with Gasserian ganglion of the Vth; the geniculate ganglion persists.	The ganglia of the facial nerve, as in the frog.
	The branches of the facial nerve are:— Ophthalmic, buccal, external mandibular (sensory), hyo-mandibular (mixed), palatine, and chorda tympani (sensory).	The branches of the facial nerve are:— Hyo-mandibular (motor), palatine, and chorda tympani (sensory).	The branches of the facial nerve are:— Hyo-mandibular (motor), palatine, and chorda tympani (sensory).
Glosso-pharyngeal. IX.	The glosso-pharyngeal supplies the wall of the first gill-cleft (mixed).	The glosso-pharyngeal supplies the wall of the first gill-cleft in the tadpole; and in the frog, the tongue and pharynx (mixed).	The glosso-pharyngeal supplies the pharynx and the tongue (mixed).

	Dogfish.	Frog.	Rabbit.
Vagus. X.	The branches of the vagus are:—Branchial, lateral line, and visceral.	The branches of the vagus in the tadpole are as in the dogfish; in the adult frog only the visceral branch remains.	Only the visceral branch of the vagus is represented.
	The vagus is the last cranial nerve.	The vagus is the last cranial nerve, and the hypoglossal is the first spinal.	The spinal accessory and hypoglossal are additional cranial nerves. The hypoglossal is the last cranial, but in its mode of development is like a spinal nerve.
Spinal nerves. Origin.	The roots of the spinal nerves alternate.	The roots of the spinal nerves arise in the same transverse plane.	The roots of the spinal nerves arise in the same transverse plane.
Regions.	No distinction into regions can be made.	The spinal nerves may be distinguished as:—8, pre-sacral; and 2, post-sacral.	The spinal nerves may be distinguished as:— 8, cervical; 12, thoracic; 7, lumbar; 4, sacral; and 15, caudal.
Brachial plexus.	No definite plexus formed.	The brachial plexus is formed by the 2nd and 3rd pre-sacral nerves.	The brachial plexus is formed by the 5th to 8th cervical and the 1st thoracic nerves.
Sciatic plexus.	No definite plexus formed.	The sciatic plexus is formed by the 7th to 10th spinal nerves.	The sciatic (lumbo-sacral) plexus is formed by the 5th to 7th lumbar and 1st to 3rd sacral nerves.

The Sensory Organs.

Eye.

The essential and sensory portion of the eye, i.e. the retina, arises as an outgrowth of the fore-brain; the lens as a thickening of the epiblast, and the other structures, such as the coats and muscles of the eyeball, from the mesoblast.

The eye of all Vertebrates from the fishes upwards is fundamentally the same, and only differs among the different classes in small though important details, so that we shall first describe a Vertebrate eye in general terms and subsequently indicate the more important differences between that of the dogfish, frog, and rabbit.

The external coat or **sclerotic** (Fig. 39, SCL) of the Vertebrate eye is a tough fibrous or cartilaginous capsule, the substance of which in

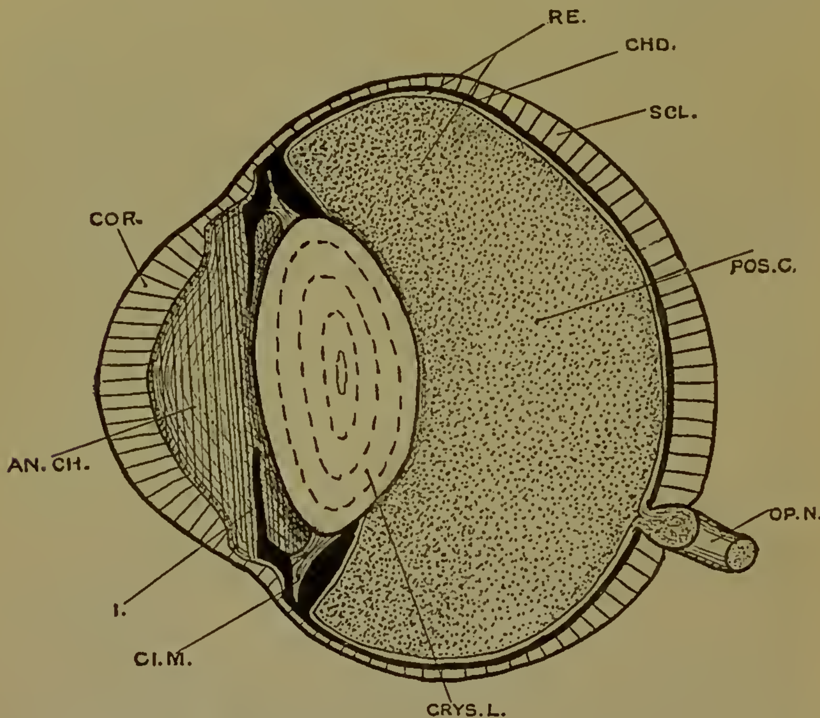


FIG. 39. Median vertical section of the eye of Ox. Other than with respect to size and form of pupil it is identical with that of the rabbit. AN.CH = anterior chamber; CRYS.L = crystalline lens; CI.M = ciliary muscle; the ciliary processes are represented by the black mass behind it; CHD = choroid coat; COR = cornea; I = iris; OP.N = optic nerve; POS.C = posterior chamber; RE = retina; one of the two index lines points to its cut edge and the other to its inner surface; SCL = sclerotic coat.

the portion that covers the front of the eye is modified to form a clear transparent material called the **cornea** (Fig. 39, COR). Within the sclerotic is the **choroid** (CHD), a highly vascular coat containing a large number of pigment cells; just behind the lens, it forms the **ciliary processes**, and extends forward to the front of the lens as a perforated curtain, the **iris** (Fig. 39, I), the size of the aperture of which is capable of variation in accordance with the varying

intensity of the light entering the eye. The **crystalline lens** (Fig. 39, CRYS.L) is a transparent body composed of a highly refractive material, and bi-convex in form; it is situated just behind the iris, and divides the globular cavity of the eye into two chambers, an anterior (AN.CH), containing a watery liquid, the **aqueous humour**, and a posterior (POS.C), containing a gelatinous fluid, the **vitreous humour**. These chambers are of the nature of lymph spaces. The lens is compressible within limits, and is invested in an elastic capsule that may be stretched, and the convexity of the lens therefore lessened, by a circularly disposed muscle, the **ciliary muscle** (CI.M).

The most internal layer is the **retina** (Fig. 39, RE), the minute structure of which is very complex, and into which two sets of elements enter, a supporting delicate connective tissue, and a sensory nervous composed of nerve-cells and their processes. The retina lines the cavity of the posterior chamber and ends abruptly in front at the point where the ciliary processes arise from the choroid. A little below and to the inner side of the centre of the back of the eyeball, the **optic nerve** (OP. N) perforates its walls and, passing through to the internal surface (that facing the posterior chamber) of the retina, radially disposes its fibres over that; they thus form a layer which is situated between the inner surface of the retina and the vitreous humour filling the posterior chamber; but they are separated from the latter by a very delicate and thin membrane, the **membrana limitans interna (hyaloid membrane)**. Exactly in the centre of the retina is a slight eminence, the **yellow spot**, with a depression in its middle, the **fovea centralis**; this lies in the axis of vision, and experimental observation has shown that it is at this spot that the sense of vision is strongest.

The retina is composed of large nerve-cells and certain other nerve structures, the whole being supported by a framework of connective tissue, of which the latter plays no part in vision, and will not, therefore, be described.

Structure of Retina. The hyaloid membrane limiting the retina internally is in reality part of the vitreous humour, so that the most internal layer of the retina is that of the fibres of the optic nerve, which become continuous with large multipolar ganglion cells of the next outer layer, which in its turn is succeeded by a granular-looking layer (**molecular layer**), composed of the much branched processes (dendrons) of the ganglion cells just described. Immediately outside this is the **internal granular layer**, composed of comparatively small bipolar nerve-cells, each of which possesses two processes, one running

inwards and the other outwards; the former branches very much to form a dendron which is contiguous to that of one of the ganglion cells of the optic fibres, while the latter also branches, and passes outwards into the next two layers, where it forms dendrous processes. The next layer is the **external molecular layer**, consisting of stellate ganglion cells and their branching dendrons, some of which are contiguous with those of the bipolar cells, while others passing inwards become contiguous with those of the multipolar ganglion cells of the optic fibres. The next layer is called the **outer granular layer** and is composed of bipolar cells with differentiated protoplasm; the outer processes of these cells pass into the outer molecular layer, and of the inner processes, some become continuous with the **rods** and others with the **cones** of the next layer, i.e. that of the **rods** and **cones**; this is in its turn limited by the **membrana limitans externa.**

The point at which the fibres of the optic nerve emerge upon the inner surface of the retina is called the **blind spot**, because light falling upon this spot is incapable of exciting the sensation of vision; the fibres of the optic nerve, therefore, are not stimulated by light, so that it is not they which receive and convert the actinic rays; but since, if the optic nerve be injured, no sensation of light is excited in the brain, they must play the part of a conductor, carrying to the brain the stimuli set in motion by the impact of the rays of light upon the retina.

The fovea centralis, as already mentioned, is a depression in the retina, and this is formed by the thinning out of all the layers of the retina except that of the rods and cones; and since the fovea centralis is the region of most acute vision, it follows that it is the layer of the rods and cones which are stimulated by the rays of light, the other layers being concerned in receiving the converted stimulus from them, which they in their turn pass on to the optic fibres, and these to the visual centre in the brain.

The features that distinguish the eye of the dogfish from that of the higher Vertebrates is the slight convexity of the cornea and the globular form of the crystalline lens, so that in front it is in contact with the cornea and behind approximates to the retina, both anterior and posterior chambers being encroached upon by it to a greater extent than in other Vertebrates. The globular form of the lens and the slight convexity of the cornea are characteristic of the eye of all aquatic animals, and the lens of such has a higher refractive index than that of terrestrial animals. The sclerotic is cartilaginous and not fibrous.

The eye of the frog resembles that of the dogfish, but is simpler in several characters, and rounder in form; the aperture of the pupil is round, not slit-like as in the dogfish.

In the rabbit the eyeball is more protected by the deep bony orbit than it is in the frog or dogfish, in correlation with which the sclerotic is no longer cartilaginous, but fibrous in character. The crystalline lens is bi-convex, not globular, and the outer surface is less convex than the inner. The form of the eyeball is more round than that of the dogfish or the frog, and the pupil is circular, but in other mammals may be vertically slit-like (cat) or transversely oval (ox, sheep, &c.).

The Ear.

Auditory Organ.

The auditory organ in the Mammalia is composed of an **external**, **middle**, and **internal ear**, of which the last, sometimes called the **membranous labyrinth**, is the essential portion, the others being accessory only to the sense of hearing. Of these parts, the internal ear arises as an ectodermic invagination (Fig. 94, A), the middle ear as an expanded portion of the Eustachian tube (a modified gill-cleft, cp. p. 161), and the external ear as an outgrowth from the mesoblast.

The membranous labyrinth is the only portion that is present in the ear of the dogfish; in the frog there is in addition the middle ear, with its related tympanic membrane and Eustachian tube; in the rabbit the middle ear is more complex than that of the frog, since some portion of the mandibular and hyoid arches (ante, p. 62) has become modified to form two of the three auditory ossicles.

The ectodermic invagination which gives rise to the membranous labyrinth becomes constricted off from the skin, and forms a round vesicle lying just beneath that (Fig. 94, A′). After a time it sinks deeper into the mesoblast and becomes constricted into two parts, of which the upper gives origin to the semicircular canals (S), and the lower (A′) to the sacculus and its related parts.

Dogfish or **Skate.** The **sacculus** or **vestibule** (Fig. 40, S) is a laterally compressed oval sac, containing milky calcareous concretions; dorsally it is continued towards the roof of the skull by a small tubular structure, the **ductus endolymphaticus** (D.E), which at its dorsal extremity is slightly dilated to form the **saccus endolymphaticus** (S.E), which opens to the exterior, at the posterior fontanelle of the

cranium, by a small aperture. The ductus endolymphaticus is the tube that arises when the auditory vesicle, instead of becoming completely constricted off from the epiblast, retains a permanent opening to the exterior; this aperture becomes elongated into a tube, as the vesicle sinks deeper into the mesoblast.

The **semicircular canals** are three in number and are arranged in the three directions of space, viz. each one is at a right angle to the other two. The **anterior** (ANT. C) and **horizontal** (H. C) **semicircular canals** open at either end into a tubular organ, the **utriculus** (U); at one end, just before their junction with the utriculus, each canal bears a dilation (AM), called the **ampulla**, and which bears internally

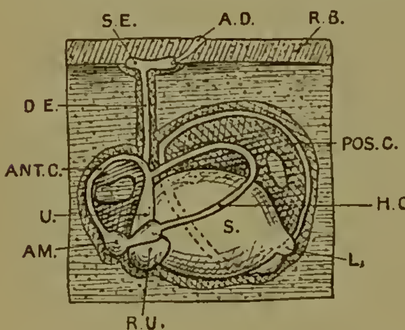


FIG. 40.

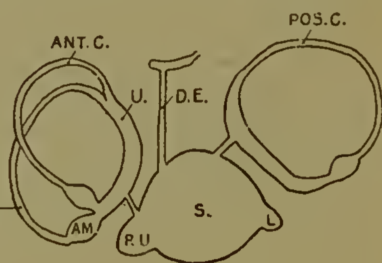


FIG. 41.

The internal labyrinth (auditory organ) of Skate. The ear of the skate has been chosen since it is larger, but it is otherwise identical with that of the dogfish. Fig. 40 represents the membranous labyrinth lying in the auditory capsule, which has been opened in order to reveal it. Fig. 41 represents it dissected out and with its parts separated. A.D = aperture of D.E; AM = ampulla; ANT.C = anterior semicircular canal; D.E = ductus endolymphaticus; H.C = horizontal semicircular canal; L = lagena; POS.C = posterior semicircular canal; R B = roof of the brain-case; R.U = recessus vestibuli; S = sacculus; S.E = saccus endolymphaticus; U = utriculus.

a modified epithelium, covered with auditory hairs; the epithelium is in connexion with nerve fibres derived from the auditory nerve. The utriculus is in communication, by means of a very small tubular canal, with a sac-like recess of the sacculus, called the **recessus vestibuli** (Fig. 41, R.U). The posterior semicircular canal opens at either end into a utricle of its own, and possesses its own ampulla at its posterior and inferior end; its utricle opens into the postero-dorsal surface of the sacculus, by a small tubular canal.

A little way behind the point at which the posterior canal enters the sacculus, there is developed a small bud-like evagination of that, the **lagena** (L).

The auditory nerve upon penetrating the inner wall of the auditory

capsule breaks up into branches, some of which pass to the ampullæ and others to the sacculus.

The whole of this complex apparatus, called the **membranous labyrinth**, is embedded in the cartilage forming the auditory capsule, which is accurately moulded to its form (Fig. 36).

Frog. The ear in this animal is divisible into two parts, the **tympanum** or **middle ear** and the membranous labyrinth or **internal ear.** The latter part is lodged in the auditory capsule, the anterior, ventral, and dorsal wall of which is ossified to form the pro-otic bone, while the posterior wall is formed by part of the exoccipital. The middle ear is a cavity bounded internally by the posterior wall of the auditory capsule and externally by the **tympanic membrane**, a rounded oval membrane lying immediately below and behind the eye, composed of radiating fibres of connective tissue, and lined internally by a layer of columnar epithelium. The middle ear communicates with the pharyngo-oral (buccal) cavity by means of the short Eustachian tube (Fig. 43, EA. AP).

In the posterior wall of the auditory capsule, there is a small opening, the **fenestra ovalis**, which is closed externally by a rod-like bone, cartilaginous at either extremity, called the **columella auris.** This bone is attached at one end to the rim of the fenestra ovalis by connective tissue, and passing across the tympanic cavity becomes attached at its other end to the tympanic membrane.

The membranous labyrinth does not completely fill the cavity of the auditory capsule, and the space thus formed, lying between the walls of the two structures, is called the **perilymphatic space**; it is filled with fluid, the **perilymph.** When the tympanic membrane is set vibrating, by sound waves impinging upon it, the columella is carried backwards and forwards by the vibrating membrane, and this in turn sets the perilymph vibrating, which then reacts upon the membranous walls of the labyrinth, which thus set the endolymph in action and this the auditory hairs.

The membranous labyrinth of the frog is very similar to that of the dogfish, but the ductus endolymphaticus and the saccus endolymphaticus, instead of opening to the exterior, pass to the cranial cavity, where the latter structure lies between the wall of the cranium and the surface of the brain. It is continued backwards, as an unpaired structure, along the whole length of the vertebral canal dorsad of the spinal cord, and gives off paired outgrowths which pass through the inter-vertebral foramina to lie upon the ganglia of the spinal nerves.

The whole structure is easily recognized by the opaque white colour due to the calcareous concretions which it contains. As in the dogfish, the recessus utriculus contains an **otolith**, a glassy homogeneous plate with striated border; it covers the whole of the patch at which one of the branches of the auditory nerve enters. In addition to the lagena present in the dogfish, there is another small oval pocket-like protuberance of the sacculus, the **pars basilaris cochleæ**, which lies immediately above and behind the lagena, and which communicates with the sacculus by an aperture common to it and the lagena. It corresponds to, and foreshadows the formation of, the basilar membrane of the cochleæ of higher forms. A little in front and above the pars basilaris cochleæ, there is another small saccular outgrowth of the sacculus, called the **pars neglecta**.

The lagena (in the frog usually called the lagena cochlea), pars basilaris cochlea, and pars neglecta, together represent a rudimentary **cochlea**, which reaches its highest stage of development in the Mammalia. All connecting stages between the rudimentary organ in the amphibian and the finished one of the mammal are to be seen among reptiles and birds; and indeed, that of the lowest mammal possesses some reptilian characters.

Rabbit. The principal differences that exist between the internal ear of the rabbit and that of the frog are connected with the obliteration of the direct opening between the utriculus and sacculus, which now only open indirectly through the forked ductus endolymphaticus, one prong of which opens into the utriculus and the other into the sacculus. Relatively to other portions of the ear, the sacculus is much smaller. The saccus endolymphaticus lies in the cranial cavity between the dura mater and the brain.

The characteristic feature of the mammalian ear is the great development of the **cochlea**, which is very much lengthened and coiled upon itself in a number of coils, which varies for different mammals. In the rabbit there are two and a half coils, in the pig almost four, in the cat three, and in man between two and a half and three coils.

The membranous labyrinth lies embedded in the bony substance of the periotic bone, the internal cavity of which is accurately moulded to the form of the labyrinth. The coiled portion of the bony capsule in which the membranous cochlea lies is not just a simple tube, but a tube with a bony shelf (**lamina spiralis ossea**) projecting inwards nearly halfway across the middle of its cavity. The membranous

cochlea is not cylindrical in form, but is rather of the nature of a triangular tube, and is so disposed within the bony one that one edge of its triangle is fastened to that of the bony shelf, its base being attached to a portion of the outer wall of the bony tube. It results from this that the lumen of the bony cochlea is divided into two compartments, which, with that of the membranous tube, are named the **scala vestibuli**, **scala media** (cavity of the membranous cochlea), and **scala tympani**. Of these, the scala media ends blindly at its extremity, at the apex of the coil, while the two others communicate with each other round its blind end. At the base of the coil, the scala tympani and scala vestibuli are continuous with the perilymphatic space between the membranous labyrinth and the walls of the bony capsule.

The lymph space of the scala tympani, and through it the perilymphatic spaces of the other parts of the ear, are in connexion with the lymph spaces of the head through a small canal, the **ductus perilymphaticus**, which leads from the scala tympani just before that ends at the **fenestra rotunda**, which is a foramen closed by membrane that faces the Eustachian tube. Higher up, in the expansion of the Eustachian tube that constitutes the compartment of the middle ear, there is another foramen, the **fenestra ovalis**, which is closed by a membrane that holds back the perilymphatic fluid of the internal ear, and gives attachment to one of the auditory ossicles, the **stapes**. The stapes, together with two other auditory ossicles, the **incus** and **malleus**, bridges the cavity of the middle ear, the latter bone being attached to the internal surface of the tympanic membrane, which is stretched across the inner extremity of the external meatus.

The floor of the scala media is composed of a membrane which is wide at the beginning (base) of the cochlea and gradually narrows as it reaches the apex. Careful microscopical examination reveals the fact that this membrane, the **basilar membrane**, is composed of a great number of fibres transversely arranged across its length, so that the vibration period of those at the base of the cochlea is longer than those at its apex. Situated upon its internal surface (that turned towards the lumen of the scala media) are some elongated **auditory cells**, the free extremities of which contain minute hair-like processes; supporting these are two rows of peculiarly shaped cells, the **bacilli** or **rods of Corti**. Overhanging the auditory cells is a thickened membrane, the **membrane of Corti**, free along its inner margin but attached to the **membrane of Reissner** or roof of the

scala tympani along the other; obviously such a membrane is free, under certain conditions, to vibrate in such a way that it might alternately be depressed upon and elevated from the hair-like processes of the auditory cells, and through them affect the vibration of the fibres of the basilar membrane.

The auditory cells and the basilar membrane are supplied by a branch of the auditory nerve, which enters the membranous cochlea through the lamina spiralis ossea, first expanding in such a way that nerve fibres enter along the whole length of the bony lamina.

A discussion of the physiology of the different portions of the ear is outside our present purpose, but the student desirous of considering the physiological nature of this organ cannot find a more succinct account than that given in Dr. Waller's *Introduction to Human Physiology*[1].

The morphological features that distinguish the mammalian ear from that of the frog or dogfish are the presence of the external ear, indications of which begin to be seen in reptiles and birds, and the high stage of development and complex structure of the cochlea.

Tabulation of the Chief Characters of the Auditory Apparatus.

Dogfish.	Frog.	Rabbit.
Auditory capsule cartilaginous and not perforated by a fenestra ovalis or rotunda.	Auditory capsule partly osseous and partly cartilaginous; perforated by a fenestra ovalis, and, in most Amphibia, also by a fenestra rotunda.	Auditory capsule is entirely osseous, and is perforated by both a fenestra ovalis and a fenestra rotunda.
There is no middle ear; the morphological representative of this is the spiracle.	There is a middle ear, formed by an expansion of the very short Eustachian recess, and bridged only by a single auditory ossicle, the columella auris.	There is a middle ear, formed by an expansion of the Eustachian tube, and containing three auditory ossicles—the stapes, incus, and malleus.
There is no external ear.	There is no external ear.	There is an external ear formed by the external auditory meatus and the pinna of the ear.

[1] Longmans, Green & Co.

Dogfish.	Frog.	Rabbit.
There is no cochlea, but its rudiment is represented in the form of the lagena.	The rudiments of the cochlea are more developed, and consist of a lagena cochlea, pars basilaris cochlea, and pars neglecta.	The cochlea reaches its highest stage of development and becomes spirally coiled upon itself. It essentially consists of stretched fibres, with graduated vibration periods.
The utriculus and sacculus open directly into each other by the utriculo-saccular canal.	As in the dogfish.	The utriculus and sacculus only open indirectly into each other by means of the forked ductus endolymphaticus.
The sacculus is relatively large.	The sacculus is relatively smaller than in the dogfish.	The sacculus is very small and has become constricted off from the utriculus.

THE NOSE OR OLFACTORY ORGAN.

The epithelium of the olfactory organ arises in all Vertebrates as an invagination of the ectoderm which forms a pit, the opening of which, becoming narrowed, persists as the **anterior nares**. The wall of the olfactory pit becomes folded and gives rise to a complicated arrangement, the object of which is to increase the sensory surface, and from the Amphibia onwards a ventral diverticulum of the pit gives rise to a special organ, the **organ of Jacobson**, which in the Mammalia acquires an opening into the mouth.

In most fishes the nose is purely a sensory organ, but from the Amphibia upwards it becomes secondarily connected with the respiratory functions by the formation of a **posterior nares** or opening into the oro-pharyngeal chamber. Upon the assumption of a respiratory function in addition to the primitive sensory one, the epithelium lining the olfactory capsule becomes differentiated into sensory and mucous cells.

Dogfish. The form of the olfactory organ in the dogfish is of the simplest type, since it consists of a pair of spherical chambers, the **olfactory capsules** (Fig. 36), lined with olfactory epithelium (OL.EP), and opening to the exterior by a pair of apertures on the ventral surface of the head (Fig. 25, N). These apertures correspond to the

anterior nares of higher forms, and the secondary connexion with the mouth by means of the posterior nares is not established. In *Scyllium canicula* the anterior nares are connected with the mouth by a pair of grooves, but these are absent in other dogfishes.

The epithelium of the olfactory chamber is thrown into a number of folds which radiate towards the centre of the capsule (Fig. 36, OL.OP).

Frog. In the frog the anterior nares open to the dorsal surface of the head, and a connexion with the oro-pharyngeal chamber is established by means of a pair of posterior nares which open just at the outer side of the vomers (Fig. 43, NAR). The apertures of the posterior nares are guarded by folds of the mucous membrane, which are so disposed that they allow air freely to enter the oro-pharyngeal cavity but prevent it from returning.

The cartilaginous olfactory capsules are bounded above by the dorsal wall of the sphenethmoid and the nasal bones, in front by the premaxillæ, below by the vomers and palatine, and at the sides by the maxillary bones. Internally each capsule is limited in the middle line by a vertical septum attached to the sphenethmoid.

Each capsule is divided by projections of the cartilaginous wall into a **superior sinus**, an **inferior sinus**, a **maxillary sinus**, and a **lateral sinus**. The maxillary sinus represents a rudimentary organ of Jacobson.

The greater portion of the olfactory chamber is lined with columnar ciliated epithelium, together with the true sensory (olfactory) cells. The epithelial cells consist of ordinary columnar cells, the free extremities of which bear cilia, and the bases of which are produced into irregularly branching processes. The sensory olfactory cells have an oval nucleated body produced at either extremity into a thicker peripheral process, which, at the general surface of the epithelium, gives origin to from five to eight stiff cilia, and a thinner peripheral process which ultimately becomes connected with the fibrils of the olfactory nerves.

Rabbit. In the rabbit the olfactory chamber is much divided by the formation of scroll-like bones, the ethmo- and maxillo-turbinals, and moreover, the posterior nares are carried far back by the formation of a narial (naso-palatine) passage, which arises as the result of the formation of the palatal processes of the maxilla and palatine (hard palate).

The anterior portion of the nasal chamber, i. e. that composed of the

maxillo-turbinal, is not olfactory, since the epithelium lining it contains no olfactory cells, and is concerned wholly with the respiratory function, tending to warm the incoming air and in part, perhaps, also to perceive of its temperature and moisture. The olfactory or sensory portion of the epithelium is confined to that lining the ethmo-turbinals.

The organ of Jacobson is quite constricted off from the nasal chamber and forms a pair of tubular organs lying at the base of the septum nasi. Posteriorly a branch of the olfactory nerve enters it and anteriorly it communicates with the mouth through the naso-palatine canals. In the rabbit, though well developed, it is somewhat reduced when compared to the stage of development which it attains in some of the lower Mammalia (Monotremes).

CHAPTER VI

ORGANS OF NUTRITION

The Alimentary Canal.

The alimentary canal is, primitively, a tubular organ extending from the mouth to the anus, and from which paired or single diverticula grow out that ultimately become organs of respiration and digestive glands. The thyroid gland arises as a diverticulum of the pharyngeal region of the canal ; the salivary glands as outgrowths of the buccal cavity of the mouth ; the lungs as an outgrowth of the œsophagus ; the liver and pancreas as diverticula of that portion of the canal which succeeds the dilation that later becomes the stomach. Gill-clefts arise as lateral pouches of the pharyngeal region of the alimentary canal, which growing outwards ultimately pierce the skin and open to the exterior.

The wall of the alimentary canal along its whole course is composed of four layers : an outer investing **peritoneal layer**, formed by the reflected peritoneum ; a **muscular layer**, consisting of muscle fibres longitudinally and circularly, and in parts obliquely arranged ; within this a **sub-mucous coat**, made up of connective tissue loosely arranged, the spaces of which are filled with wandering lymph corpuscles, and in which the blood-vessels, lymphatics, and nerves supplying the alimentary wall anastomose ; and innermost of all, the **mucous layer**, lining the cavity of the canal, and consisting of an epithelium, supported upon

a very thin layer of muscular fibres, and the nature of which varies from region to region. Tubular evaginations of this epithelium, which are microscopic and always confined to the thickness of the wall, form glands of more or less complexity, the function of which is the production of some of the digestive juices from the blood-stream flowing through the capillaries that are in close relation to them.

Of the various layers of the alimentary wall, the epithelial is derived from the hypoblastic germinal layer, and the remaining ones from the mesoblast. The epithelium lining the cavity of the greater part of the mouth and the basal portion of the rectum is of epiblastic origin, since these regions are formed by invaginations of the outer skin, and secondarily become connected with the cavity of the alimentary canal.

Dogfish. The mouth is a large crescentic aperture, situated on the under surface of the head, a little way behind its anterior extremity; it is continued inwards as a wide slit-like **buccal cavity** (Fig. 42, B.C), which becomes continuous with a more spacious one, broad from side to side, but narrow from back to front, the walls of which are perforated on either side by five vertical gill-clefts that place it in communication with the exterior. This cavity is a common passage for the food and water, the latter of which, taken in at the mouth, passes out through the gill-clefts for purposes of respiration. This region of the alimentary canal, common to the passage of nutritive and respiratory materials, is called the **pharynx** (Fig. 42, P).

Teeth. These are very simple in form, being merely conical bodies, with a four or three-rayed base, by means of which they are embedded in the skin covering the upper and lower jaws; they are but the enlarged scales which everywhere are embedded in the skin of the trunk. The main portion of the tooth is composed of a bony material, but which has not the structure of bone, and is called **dentine**; the apex of the cone (pointed extremity of the tooth) is capped by a very hard, dense, almost wholly mineral substance, called **enamel**. In the middle of the tooth is a **pulp-cavity**.

The teeth of the dogfish are all of one form, and hence the dentition is said to be **homodont**.

The pharynx narrows posteriorly and passes into a large tubular organ, which is situated in the middle line and dorsad of the heart; this is the **œsophagus** (Fig. 42, Œ), and at its posterior end it dilates and passes into a U-shaped **stomach** (S), the proximal limb of which (that continuous with the œsophagus) is much wider than its distal loop (D.L.S). This portion of the stomach is continued into the

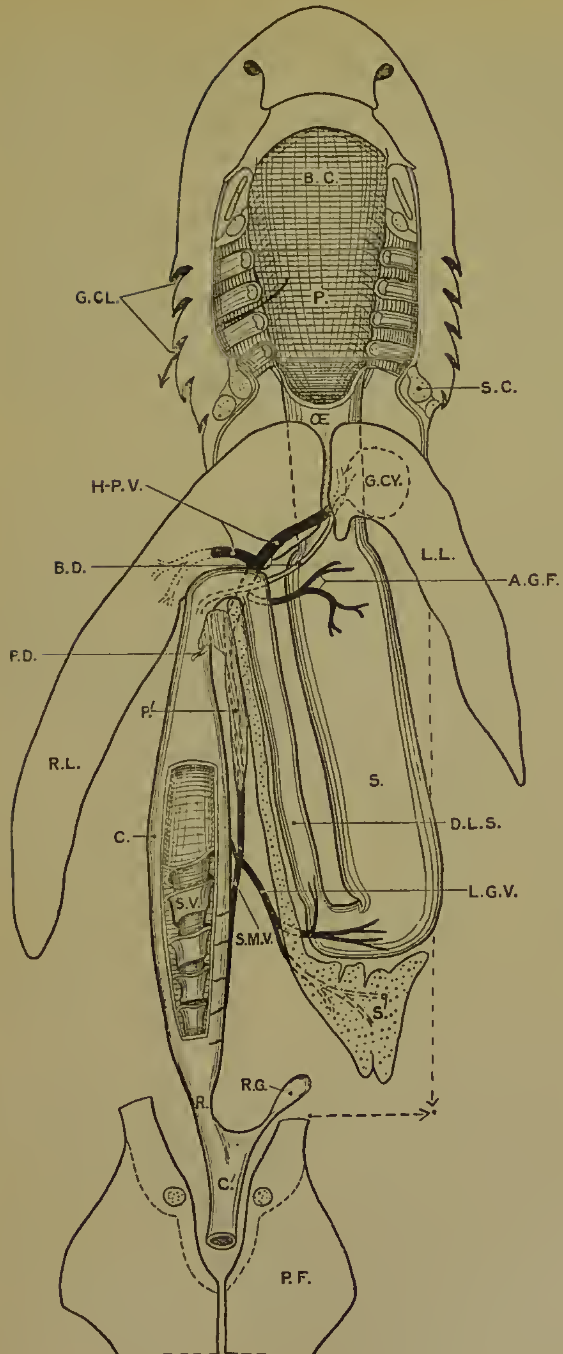


FIG. 42. Ventral dissection of Dogfish (*Scyllium*), to show alimentary canal and hepatic-portal system. The ventral body-wall, shoulder-girdle, and heart have been removed. In order not to obscure clearness by representing tbe parts too close together, tbe colon has been displaced a little to the right; the transverse dotted line indicates by how mucb. A.G.F = anterior gastric factor of bepatic-portal vein; B.C = buccal cavity; B.D = bile-duct; C = colon; C′ = cloaca; D.L.S = distal loop of stomach; G.CL = gill-clefts; G.CY = gall-bladder; H-P.V = hepatic-portal vein; L.L = left lobe of liver; L.G.V = lieno-gastric factor; Œ = œsophagus; P′ = pancreas; P = pharynx; P.D = pancreatic duct; P.F = pelvic fin; R = rectum; R.G = rectal gland; R.L = rigbt lobe of liver; S = stomach; S′ = spleen; S.C = supra-scapula; S.M.V = anterior mesenteric vein; S.V = spiral valve of colon.

large **intestine** or **colon** (C), which lies in the middle line of the body, follows a perfectly straight course, and, at first narrow, widens rapidly as it passes backwards, and then narrows again to become continuous with the **rectum** (R). Along its posterior two-thirds the surface of the wall of the colon is marked by a slight constriction, which follows a spiral course; this is the external indication of a spiral fold of the intestinal epithelium which, projecting into the cavity of the intestine, forms a **spiral valve** (S.V), the function of which is to enormously increase the absorptive surface of the wall without adding to its length. The portion of the intestine between the beginning of the valve and its junction with the distal loop of the stomach corresponds to the duodenum of the frog and rabbit, since it receives the bile (B.D) and pancreatic (P.D) ducts, the former upon its dorsal, and the latter upon its ventral, surface.

The **rectum** is continuous with the colon anteriorly and posteriorly with a portion of the alimentary canal which receives not only the fæces from the intestine, but also the renal and generative products. This part is called the **cloaca** (C′), and its opening to the exterior the **cloacal aperture**. Just before the rectum passes into the cloaca, it receives upon its dorsal wall a club-shaped gland, the **rectal gland** (R.G), the probable function of which is to promote the act of defæcation.

The **pancreas** (P′) is an elongated whitish organ lying between the colon and the distal loop of the stomach; its anterior end is expanded to form a small ventral lobe which lies upon the ventro-lateral surface of the colon, and from which the **pancreatic duct** (P.D) emerges to almost immediately enter the great intestine near its anterior end. The duct runs for some distance embedded in the wall of the colon before it opens to its interior, just to the outer side of the commencement of the spiral valve, so that its internal aperture is posterior to the point at which it first pierces the wall of the intestine.

The **liver** (R.L & L.L) is a yellowish organ consisting of two elongated lobes, which run almost the length of the body cavity, one on either side. Anteriorly the two lobes are larger than at their other ends, and are joined together in the middle line; their anterior ends are connected with the hepatic sinus (Fig. 25, HEP.S), into which their large, somewhat irregular, hepatic veins open. The **gall-bladder** (Fig. 42, G.CY) lies embedded in the substance of the left lobe near its anterior end, and from it a large thick-walled **bile-duct** (B.D) emerges which, after receiving several smaller ducts from both lobes of the liver,

passes in a straight course to the dorsal wall of the intestine, which it enters a little behind its anterior end. Like the pancreatic duct, the bile-duct runs for some distance within the wall of the intestine, so that its internal opening is a little posterior to its first connexion with it.

Situated at the bend of the two loops of the stomach, and extending along the right side of its distal loop, is a reddish-brown organ which, while it really belongs to the lymphatic system, may be mentioned here; it always occurs in association with some part of the alimentary tract, usually the stomach. It is one of the so-called 'ductless glands,' and is known as the **spleen** (S′); its function is uncertain.

The dogfish is a carnivorous feeder, feeding on other fish, preferring herrings, but not averse to bivalve molluscs, notwithstanding the mineral nature of their shells. The intestine of all animals is to some extent correlated to their mode of feeding, and in those instances in which the diet is of a concentrated nature, we find that the intestine is short and the cæcum rudimentary or absent. The intestine of the dogfish is of this nature, for, as we shall see, certain parts, i. e. duodenum, ileum, and cæcum, present in other animals are absent in the dogfish, unless that portion of the colon already mentioned corresponds to the duodenum.

Frog. The mouth of the frog is situated at the anterior extremity of the head, and is a wide aperture, extending from ear to ear.

Teeth. These are confined in the frog to the upper jaw and vomers. Like those of the dogfish, they are all of one form, and the dentition is, therefore, homodont.

Each tooth consists of a root with a pulp-cavity, with a basal portion above, marked off from a small crown by a circular furrow. The apical portion of the crown is bifid, and is capped by a layer of hard enamel; the remaining portion of the tooth is composed of dentine.

The internal nares open to the buccal cavity, or rather to the pharyngo-oral or pharyngo-buccal cavity, to the outer side of the vomerine teeth; each is guarded by a small fold of membrane, in such a way that air can enter the cavity freely, but upon endeavouring to pass out, closes the apertures of the nares, by pressing the membranous valves back upon them. At the hinder angle of the pharyngo-oral cavity (Fig. 43), on either side is to be seen the wide circular apertures of the **Eustachian tubes** (EA.AP), which lead directly to the cavity of the ear. The Eustachian tubes have been held to be homologous with the spiracle of the dogfish, or in other words, that they represent the vestiges of a gill-cleft; but during their develop-

ment, although they arise in close connexion with the first gill-cleft, they never at any period open to the exterior. It is doubtful, therefore, whether they have any definite relation to gill-clefts.

Behind the Eustachian tubes, the pharynx (pharyngo-oral cavity) narrows rapidly and leads to the aperture of the œsophagus (Fig. 43), ventrally to which is to be seen the slit-like aperture of the glottis (Fig. 27) in the middle of the convex eminence formed by the arytenoid cartilages (ARY) of the larynx, or the first portion of the air-tube.

The tongue (Fig. 43, T) is an extensible, evertible organ, attached by its anterior extremity to the front angle of the lower jaw; its free extremity, which in the inverted position lies in the back portion of the pharyngo-oral cavity, is markedly bifid. The tongue is an organ of taste, and as well an organ of prehension, for it can be rapidly everted from the mouth and small insects captured by its free extremities, thence carried almost to the aperture of the œsophagus upon its return to the mouth.

The **œsophagus** is a relatively long tube, passing backwards in the middle line, dorsad of the heart (Fig. 27), and bearing at its posterior end a not very marked dilation, the histological structure of the wall of which is different from that of the œsophagus. This organ is the **stomach** (Fig. 43, ST), the internal layer of which, like that of the œsophagus, is thrown into a series of longitudinal folds, by means of which the area of absorption is increased, without any increase in the size of the organ as a whole; hence these folds play in the economy of the frog's stomach the same part that the spiral valve does in the intestine of the dogfish.

The stomach lies entirely to the left of the middle line, but as it is somewhat curved in form, its two extremities lie in this line; at the pyloric extremity it passes into the **duodenum** (DUO), which is so disposed in relation to the stomach, that a U-shaped area with somewhat diverging limbs is enclosed between them. The duodenum lies more or less in the middle line, and towards the right it passes into the **ileum** or **small intestine** (Fig. 43, IL), which forms three coils and then passes into the **colon** or **large intestine** (CO), which is of much greater transverse diameter than the ileum. The mode of junction of the ileum and colon is interesting, since it foreshadows the mode of origin of the cæcum of the rabbit. An examination of Fig. 43 will reveal the fact that the ileum does not enter the colon exactly in the centre, but towards its ventral surface, and dorsally to this the anterior end of the colon is prolonged forwards

for a very short way only, as a papilliform eminence. The anatomical relation of this to the ileum and colon is precisely that of the cæcum of the rabbit; and moreover, the cæcum of the rabbit arises, in the course of its development, as a papilla-like bud, having all the anatomical relations of this eminence in the frog's intestine. There is thus present in the frog's intestine a rudiment of the cæcum, which, as we shall see, attains a very great degree of development in the rabbit. Posteriorly, the colon narrows and passes into the cloaca (CLO), and at the junction of the two, upon the ventral surface,

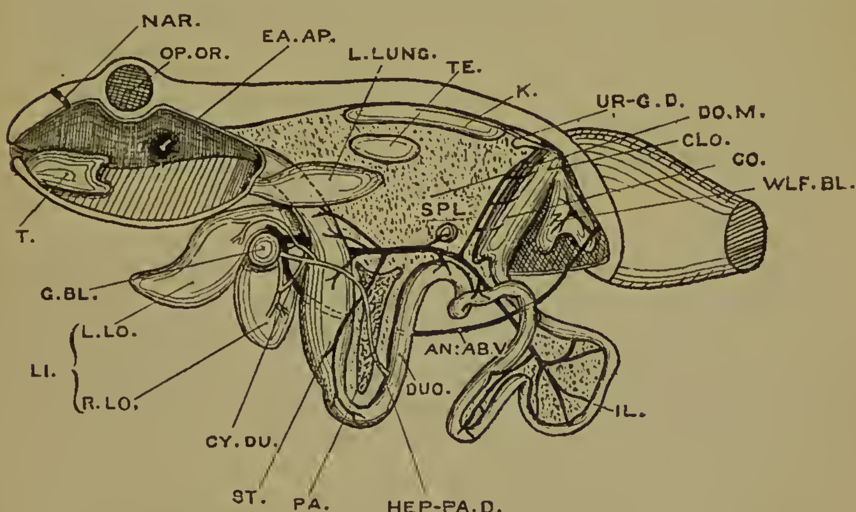


FIG. 43. Side dissection of *Rana* (Frog), to show general disposition of viscera, and the anatomy of alimentary canal and hepatic-portal blood system. AN.AB.V = anterior abdominal vein; CLO = cloaca; CO = colon; CY.DU = cystic duct; DO.M = dorsal mesentery; DUO = duodenum; EA.AP = Eustachian aperture; G.BL = gall-bladder; HEP-PA.D = hepato-pancreatic duct (common bile and pancreatic duct); IL = ileum; K = kidney; LI = liver; L.LO = left lobe of same; R.LO = right lobe of same; L.LUNG = left lung; NAR = nostril; OP.OR = orbit of eye; PA = pancreas; ST = stomach; SPL = spleen; T = tongue; UR-G.D = urino-genital duct; WLF.BL = Wolffian bladder.

the **Wolffian bladder** (WLF.BL) enters; at its free extremity, this is bilobed. Upon the dorsal wall of the cloaca, in the female, the oviducts and ureters enter, and in the male the urino-genital duct (UR-G.D).

The **spleen** (SPL) is a small, oval, reddish body situated at the anterior end of the colon, upon its dorsal surface.

The **pancreas** (PA) is a whitish compact gland, lying in the mesentery between the duodenum and stomach; its anterior end is wider than its posterior, which lies near the pyloric termination

of the stomach. Its ducts are short and enter the bile-duct (HEP-PA.D) as that passes through the pancreas to reach the dorsal surface of the duodenum.

The **liver** (LI) is divided into two lateral lobes, the anterior ends of which lie on either side of the heart, and are united by a median portion ; the left lobe (L.LO) is partially subdivided, the depth and number of incisions being very variable. The **gall-bladder** (G.BL) lies upon the posterior surface of the median portion, and it receives two **cystic ducts** (CY.DU), derived from a common bile-duct, which passes through the substance of the pancreas ; the common duct (HEP-PA.D) leaving the posterior border of the pancreas enters the duodenum obliquely, a little way beyond the junction of that with the stomach. The cystic ducts and the anterior portion of the bile-duct receive several hepatic ducts from the three lobes of the liver. As already mentioned, the bile-duct conveys both bile and pancreatic fluid, so that it is more correctly called a **hepato-pancreatic duct** (HEP-PA.D).

Rabbit. The mouth is situated at the anterior end of the head and is limited by well-defined upper and lower lips, the former of which is traversed in the middle line by a hairless tract ; the morphological nature of the cavity of the mouth (buccal cavity) is well shown by a patch of hair, like that covering the body generally, on the inner surface of either cheek ; it shows that the buccal cavity is an invaginated portion of the skin.

The respiratory and food passages have become separated by the formation of a bony plate (Fig. 20, P.PRO. & P), formed in part by median ingrowths of the palatine, and in part by similar, but broader ingrowths of the maxilla ; the dorsal passage, i. e. that along which air passes, is called the **nasal**, **naso-palatine** or **narial passage**, and the ventral, along which the food passes, and that lodges the tongue and teeth, the **buccal cavity**. In the dog these two passages are almost completely separated by the bony plate (palatine processes of the maxilla and palatine), the two portions of which are very much wider than those in the rabbit ; but in the latter the median ingrowths (palatine processes) of the maxilla and palatine are narrow, and together only form a bridge which passes from side to side between the two passages. In the living animal, however, the nasal and buccal cavities are separated by a thick membrane, which forms the roof of the latter, and anteriorly is firm and raised into transverse ridges, to form the **hard palate** ; posteriorly to this is the **soft palate**, which

is soft and smooth, and terminates behind in a notched border. Behind the notched border is a chamber into which both the nasal and buccal cavities open; this is the **pharynx**, and upon its floor is situated the **glottis** or opening of the air-tube, guarded by a flap of cartilage, the **epiglottis**. Dorsally to the glottis the pharynx passes into the œsophagus. In the hinder part of the narial chamber, the two oval apertures of the **Eustachian canals** may be seen, placing it in communication with the tympanic cavity or middle ear. In the rabbit these canals are known to be the modified hyo-mandibular gill-clefts, and therefore homologous to the spiracle of the dogfish.

The **teeth**[1] comprise an anterior and posterior pair of incisors, three pairs of premolars and molars on either side in the upper jaw. The teeth of the lower jaw are similar to those of the upper, but there is only one pair of incisors and two pairs of premolars. Between the incisors and the first premolar there is a large space without teeth, the **diastema**.

Salivary glands. These are a series of paired glands, lying in the neighbourhood of the buccal cavity and opening into it by means of ducts. They are concerned in the formation of saliva, and of the digestive ferment, ptyalin, that is capable of converting starch into sugar. They are absent in the dogfish and the frog, hence there is no mastication of the food in these animals ; and in mammals the glands sometimes do not produce the digestive ferment until some time after birth, and in man not until the sixth or ninth month. The most posterior pair are the **parotid glands**, situated at the posterior end of the mandible and ventrad of the external auditory meatus, and which open to the buccal cavity, on either side, by a small aperture near the second upper premolar, by means of the long **Stenonian duct**. The **submaxillary** and **sublingual glands** lie between the rami of the mandible and open into the floor of the mouth, the former by means of **Wharton's duct** just in front of the root of the tongue, and the latter by two ducts a little way in front of the apertures of those just mentioned. The **infra-orbital gland** lies in the orbit of the eye, and opens to the mouth near the aperture of the Stenonian duct.

The **œsophagus** is continuous anteriorly with the pharynx, and passing backwards in the middle line, behind the trachea while in the region of the neck, and behind the heart while passing through the thorax, it pierces the diaphragm and reaches the abdominal cavity,

[1] The teeth of the dog are described with the skeleton of the skull, p. 77.

where it enters the transversely elongated stomach at about the middle of its length (Fig. 44, OES). The **stomach** (S) lies with its long axis across the body cavity, a relation which only arises during the course of development, for primitively the stomach of the rabbit is like that of the frog, a mere dilation of this portion of the alimentary canal, the long axis of the dilation lying along the long axis of the body. The stomach is divisible into two regions, a **cardiac** (C.P) lying to the left of the œsophagus, and a **pyloric** (P.P) lying to the right of that; these two regions are characterized not only by differences of position and external form, but also by slight differences in the histological structure of their walls.

The **duodenum** (DUO), or first portion of the small intestine, arises from the pyloric end of the stomach, the junction between them being marked by a thickened annulus (PY) resulting from a great increase in the circular muscle fibres of the coat in that region. The duodenum (Figs. 31 & 44, DUO) forms a long U-shaped loop that extends to the posterior end of the peritoneal cavity, and anteriorly its distal limb passes into the **ileum** (Figs. 31 & 44, IL) or remaining portion of the small intestine, which is many times the length of the animal's body and is coiled upon itself in a complicated manner. Along the whole of its course oval patches of a whitish colour, characterized by the honeycombed arrangement of the small arterioles passing through them, are to be found here and there; they are composed of lymphoid tissue and are known as **Peyer's patches** (Fig. 44, PE.PA). At its posterior extremity the ileum dilates considerably and forms a large, somewhat thick-walled sac, the **sacculus rotundus** (Fig. 44, S.R), the wall of which is of the same nature as a Peyer's patch, and which opens into the large, spirally constricted blind gut or **cæcum** (CÆ). The cæcum in the rabbit is of great size and is terminated by an elongated cylindrical whitish body, which when examined microscopically, is seen to be of essentially the same nature as a Peyer's patch, and is named, from its worm-like form, the **vermiform appendix** (Fig. 44, V.A). The cæcum itself is a thin-walled sac about ten inches in length, the inner membranous coat of which is folded inwards to form a pendent **spiral valve**, that runs along its whole course, and the presence of which is marked externally by a spiral constriction of the wall. A little way in front of the junction of ileum and cæcum, the latter passes into the **colon** (CO) or **large intestine**, characterized by the sacculations of its wall being arranged in three rows that alternate with smooth areas of unequal width;

the colon quite gradually passes into the **rectum** (RE), a long thin-walled smooth tube, of about thirty inches in length, which makes two

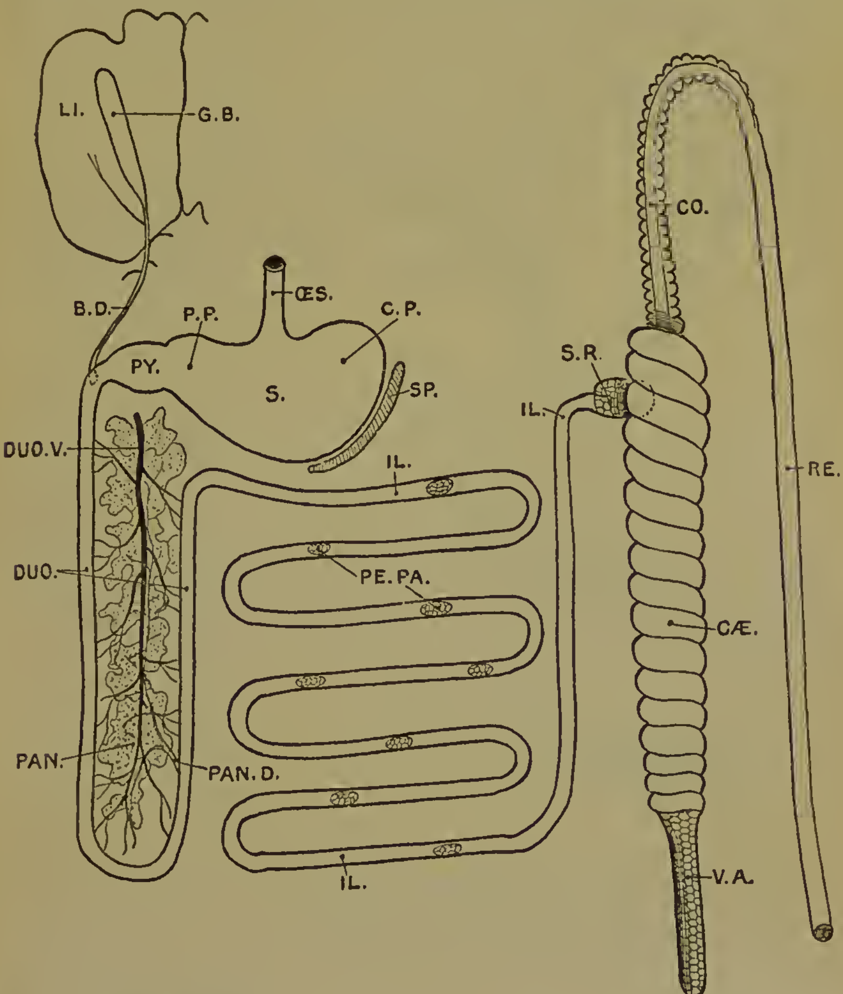


FIG. 44. Semi-diagrammatic representation of the alimentary canal of Rabbit (*Lepus*). B.D = bile-duct; CÆ = cæcum; C.P = cardiac portion of stomach; CO = colon; DUO = duodenum; DUO.V = duodenal vein; G.B = gall-bladder; IL = ileum; LI = right lobe of liver; ŒS = œsophagus; PAN = pancreas; PAN.D = pancreatic duct; PE.PA = Peyer's patches; P.P = pyloric portion of stomach; PY = pylorus; S = stomach; S.R = sacculus rotundus; SP = spleen; RE = rectum; V.A = vermiform appendix.

or three loops that run the greater portion of the length of the peritoneal cavity and ultimately pass through the pelvic cavity, to end externally at the anus.

The **pancreas** (Fig. 44, PAN) is not a compact organ like that in the dogfish and the frog, but a diffuse one, scattered about in little aggregates of lobules, in the mesentery of the U-shaped duodenum; the separate portions are connected by ductules, which uniting, ultimately form the **pancreatic duct** (PAN.D), that opens into the distal limb of the duodenum about an inch beyond the bend.

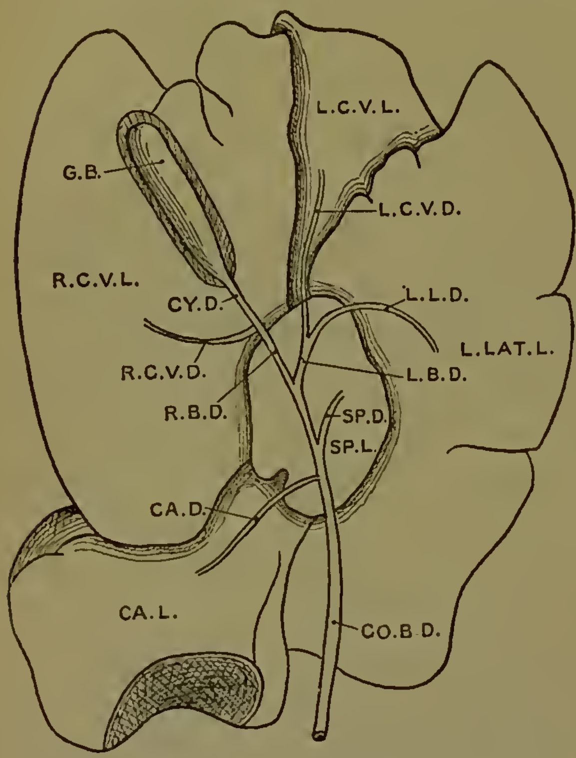


FIG. 45. Posterior aspect of liver of Rabbit (*Lepus*). CA.L = caudate lobe; CA.D = caudate duct; CO.B.D = common bile-duct; CY.D = cystic duct; G.B = gall-bladder; L.B.D = left bile-duct; L.C.V.D = left central ventral duct; L.C.V.L = left central ventral lobe; L.L.D = left lateral duct; L.LAT.L = left lateral lobe; R.B.D = right bile-duct; R.C.V.D = right central ventral duct; R.C.V.L = right central ventral lobe; SP.D = Spigellian duct; SP.L = Spigellian lobe.

The **liver** (Fig. 45) is a large organ, lying immediately behind the diaphragm, to which it is attached by a median so-called **suspensory ligament**. It is divided into five lobes, but the two primary lobes (right and left) of the liver of all Vertebrates are still distinguishable. To the right of the suspensory ligament is the **right central ventral lobe** (R.C.V.L), corresponding to the right lobe of the dogfish's or frog's liver; to the left of it is the **left central ventral lobe** (L.C.V.L), corresponding to the left lobe of the frog; and posteriorly to this is the **left lateral lobe** (L.LAT.L). The **Spigellian lobe** (SP.L) is the smallest of the five and fits into the lesser curvature of the stomach; the **caudate lobe** (CA.L) lies posteriorly to the right central ventral lobe, and has a deep concave depression on its hinder surface, which fits over the head of the right kidney.

The posterior surface of the right central ventral lobe is deeply grooved for the reception of the pyriform **gall-bladder** (G.B), which is continued backwards as a long duct (CO.B.D) that enters the duodenum upon its dorsal surface, immediately after its origin from the stomach (Fig. 44, B.D). The **common bile-duct** (Fig. 45, CO.B.D) receives two lateral ducts, i. e. the right (R.B.D) and left (L.B.D) bile-ducts, the former of which is formed by a duct (R.C.V.D) from the right central ventral lobe, and one (CY.D) from the gall-bladder ; the latter is formed by ducts from the left central ventral (L.C.V.D) and left lateral (L.L.D) lobes. The Spigellian (SP.D) and caudate (CA.D) ducts enter the common bile-duct independently.

The **spleen** (Figs. 31 & 44, SP) is an elliptical, flattened, reddish organ, lying in the mesentery upon the dorso-posterior border of the stomach.

The **thyroid**. This is a gland of unknown significance, and is one which, during the course of the phyllogeny of the Vertebrata, has undergone a remarkable change in its physiological activities. In *Amphioxus* it is probably represented by the hypo-branchial groove or endostyle (Fig. 55, END), the cells of which secrete a mucilaginous substance that agglutinates the food particles contained in the stream of water passing through the pharynx, and thus, in a way, serves as a filter, retaining the food particles and allowing the water to flow out over the gills. In the Ammocœte (larva of the lamprey) the thyroid is represented by a median sac, lined by ciliated epithelium, and lying beneath the pharynx, into which it opens between the third and fourth gill-clefts. In the adult lamprey, however, it loses its connexion with the pharynx, and gives rise to numerous closed glandular sacs, containing a mucilaginous material. In the dogfish it is a single glandular organ, having no communication with the pharynx and lying just behind the symphysis of the mandible. In the frog it is paired, each gland being oval in form, reddish coloured, and situated just in front of the posterior cornua of the hyoid bone. In the rabbit it is composed of a median lobe lying upon the ventral surface of the trachea, far forward at its anterior end, and continued backwards on either side, by an elongated lateral lobe. In all three animals the thyroid arises as a median diverticulum of the floor of the pharynx, so that at this early stage its relations are similar to those of the thyroid in the lamprey (the lowest Vertebrate above *Amphioxus*); it is only later, when it has lost its connexion with the pharynx, that it assumes the relations and positions described above.

With respect to the function of the thyroid, there is reason for believing that it is concerned in forming some material which it pours into the blood-stream, and which plays some profound, but unknown, part in the processes of metabolism; for if the gland be extirpated, it is followed by various disturbances of the mental and organic functions, most marked among which is the rapid wasting of the tissues of the body, notwithstanding the presence of abundant food material. The various consequences of extirpation disappear if the animal (man or other) be fed with extract of the thyroid gland of the sheep or pig.

The **thymus.** This is another organ of problematical nature. In the dogfish it arises as epithelial outgrowths from the upper part of the first five gill-clefts, from which later it separates and degenerates into lymphoid tissue. In the frog (tadpole stage) it arises as an epithelial bud in the dorsal roof of the first gill-cleft, from which later it separates and becomes so far differentiated that a cortical band surrounding a medulla can be distinguished. By the time of the metamorphosis it has shifted from its primitive position and lies behind the ear, on either side, as an oval body. Similar buds to those from which the thymus arise are to be found in the same position in the hyo-mandibular cleft (that in front of the first gill-cleft) and also in the second and third gill-clefts. In the rabbit the thymus is a soft pinkish mass lying in the anterior part of the thorax, and investing the roots of the pulmonary and aortic arteries. It is very variable in size, being very large in the young animal but decreasing in size as age advances, and in old animals is only represented by fat. It arises in the same way as that in the dogfish and frog, as epithelial buds of the dorsal wall of the branchial (gill) clefts, but in this particular case it arises from *one* of the hinder pouches and increases very much in size as it shifts its position backwards, subsequent to its separation from its origin.

The formation of this gland in all Vertebrates from the roof of a gill-pouch is apparently a very strange one. But we shall see, when we come to consider the development of the pharyngeal bars of *Amphioxus*, that there is primarily a series of primary bars, and from the roof of the cleft, in between any two of these, there later arises another bar, called a secondary or tongue bar (Fig. 54, C): now the origin of this bar is almost identical with that of the thymus gland in other Vertebrates. It appears, therefore, that the thymus gland is homologous to the tongue-bars of the pharynx of *Amphioxus*; and,

since it disappears in a large number of adult animals, it must be regarded as a vestigial organ in the course of disappearing.

Organs of Respiration.

With the exception of the external gills of tadpoles, which are epiblastic in origin, the organs of respiration in Vertebrates arise as outgrowths of the hypoblastic lining of the anterior part of the alimentary canal. In fishes, which breathe by means of lamellar folds of the membrane lining pouch-like clefts (Fig. 42, G.CL) of the walls of the pharynx, they arise as a series of lateral diverticula of that, which growing outwards, reach the epiblastic layer, by the absorption of which they ultimately open to the exterior. The clefts thus formed are called **gill** or **visceral clefts** (Figs. 25, 26, & 42), and the wall between any two successive clefts is supported by a cartilaginous (dogfish) or bony (cod) skeleton, called the **visceral** or **branchial arches** (Fig. 26, E.B. & P.B, & Fig. 17). In some fishes (dogfish) the clefts open independently to the exterior, but in others (cod) they open into a common chamber, formed by a fold of the integument called the operculum, which opens by a single slit-like aperture to the exterior.

In terrestrial animals and some fishes (Dipnoans) the organs of respiration take the form of paired sac-like diverticula of the œsophagus, arising from its ventral surface, but later becoming separated from it to form **lungs** (Fig. 27, L). The **air-bladder** of fishes is morphologically of the nature of lungs, arising as it does from the anterior part of the alimentary canal; but it differs from them in that it arises from the dorsal and not the ventral surface. As a rule the air-bladder acts as a hydrostatic organ, but in some cases it may function as an accessory respiratory organ.

In all Vertebrata, from Amphibia upwards, the anterior extremity of the air-tube (trachea) leading to the lungs becomes differentiated to form an organ, the **larynx**, the walls of which are supported by certain cartilages derived from the branchial arches of the embryo, and the function of which is to regulate the inflow and outflow of air to and from the lungs, and to guard the passage to them. In many cases it is further modified to act the part of a resonant organ.

Dogfish. The gills of the dogfish consist of closely-set transverse laminæ called gill-filaments (Fig. 25, G.F) attached to both sides of the gill-septum, which at its base is supported by the cartilaginous skeleton of the gill (branchial) arches, and throughout its breadth by the gill-

rays. The transverse laminæ (gill-filaments) are in reality folds of the membrane forming the gill-septum, and between the two layers of which each lamina is thus composed, there is a layer of loose connective tissue in which the blood capillaries that join the afferent and efferent branchial arteries (Figs. 25 & 26) run. So that the blood contained in the capillaries is only separated from the air-containing water flowing through the gill-slits by the thin membrane of the gill-laminæ, and the thinner membrane of the capillary walls; and it is while the blood, laden with carbon dioxide derived from the metabolism of the tissues through which it has flowed, is passing through the capillaries of the gill-laminæ, that an interchange between the gases of the blood and those of the water takes place, some of the carbon dioxide of the blood passing out to the water, and some of the oxygen of the water passing into the blood. The process is doubtless, to a large extent, a physical one of osmosis controlled by the peculiar powers of the living epithelium.

The afferent branchial artery enters the gill-septum at its base and in the middle line, and runs along the inner surface of the cartilaginous gill-arch for the whole length of the gill; along its course, it gives off, right and left, a series of capillaries which pass from end to end of the gill-laminæ, thence turning round and passing backwards, they enter the factors of the efferent branchial arteries which lie on either side of the gill-septum.

The gill-septum, with the gill-laminæ of both its posterior and anterior face, is called a **holobranch** or **gill**, and the gill-laminæ on either surface of the septum is called a **hemibranch** or **half gill.** In the dogfish the hyoidean arch (Fig. 25, HY.A) bears a hemibranch on its posterior surface, the first four branchial arches each bear a holobranch, and the last branchial arch none at all.

Frog. From the period of hatching up to that immediately preceding the formation of the mouth, the tadpole of the frog breathes by means of plumose tubular outgrowths of the skin, situated on the first to third branchial arches; in each lobe of these external gills a looped blood-vessel is contained, one limb of which is afferent, carrying blood to the gill, and the other is efferent, carrying it inwards to the dorsal aorta. Subsequent to the formation of the mouth, the gill-clefts appear, and upon their surfaces the internal gills are developed; these persist until the period of the metamorphosis, and upon their appearance the external gills disappear. At the metamorphosis the lungs are fully formed and functionally active, but long before this they

have been developing and have been used for purposes of respiration to a partial extent.

The frog therefore, during its life, breathes by means of three distinct sets of organs:—the **external gills** of epiblastic origin; the **internal gills** of hypoblastic origin, arising like those of fishes; and from the period which marks the end of the tadpole throughout life, by means of **lungs.** The **lungs** (Fig. 27, L) are paired and open to the pharynx by a single aperture, the **glottis**, which is situated at the anterior end of a membranous sac, called the **larynx**, the walls of which are supported by cartilage. The aperture of the glottis is supported by the paired **arytenoid cartilages** (Fig. 27, ARY), one on either side, while the upper portion of the laryngo-tracheal chamber is supported by a ring-like cartilage, the **cricoid** (Fig. 27, C.CAR) and its processes.

The lungs are attached at the posterior border of the cricoid cartilage, one on either side of the median plane, and are at first tubular, but soon dilate to form a sac-like organ, which lies on either side of and behind the heart. They are simple membranous sacs, the walls of which are not folded, although their internal surface is raised into ridges, which are arranged in a coarse network; the larger blood-vessels and the muscle fibres of the lungs run within these ridges. Internally the lungs are covered by a thin membrane, composed of flattened tesselated cells supported by a basement membrane. The branches derived from the pulmonary artery form a network of capillaries which traverse the wall of the lungs, and open ultimately into the pulmonary veins. While the blood passes through the capillaries it gives up its CO_2 and takes up O.

Rabbit. The lungs of the rabbit are very complex in their minute structure, a complexity which arises from the almost infinite number of times that the wall of the primitive sac-like organ (as seen in the lung of the frog) has been reduplicated in order to form a large number of such primitive sacs, each of which is called an **infundibulum.**

The lungs are two in number, one on either side of the thoracic cavity (Fig. 46), of which the right is larger than the left. They are suspended by their roots, formed by the entry of the bronchial tubes (R.BRO & L.BRO) and pulmonary artery (PU.A) into them, but elsewhere they are quite free from any attachment.

The windpipe or **trachea** (Fig. 46, TR) passes down along the ventral surface of the neck, in the middle line (Fig. 38), to enter the thorax; here it divides into two **bronchi**, one to the right (R.BRO) and

the other to the left (L.BRO), which enter the right and left lung respectively. Within each lung each bronchus gives off two lateral rows of smaller bronchi, which by further subdivision give rise to a great number of very small **bronchioles**, at the ultimate termination of each of which there is borne a triangular membranous air-sac, called the **infundibulum**. The pulmonary arteries (PU.A) enter the lung along with the two main bronchi, and follow their ramifications, the branching of the arteries corresponding with that of the bronchi. The capillaries resulting from the ultimate branching of the arteries form a very close meshwork over the surface of the infundibuli, so close that the interval between any two capillaries is less than the width of either of the capillaries themselves. The blood is thus separated from the air contained in the infundibuli, which is brought to them through the trachea and bronchi, only by their exceedingly thin membranous walls and those of the capillaries, and which together are barely thicker than the film of a soap-bubble. And it is while the blood is passing through these capillaries that an interchange between its contained CO_2 and the O of the air in the infundibuli is effected. By the union of the capillaries derived from the branching of the pulmonary arteries, the factors of the pulmonary veins are formed, and these return the arterialized (oxygenated) blood to the left auricle of the heart.

A careful comparative examination of the arrangement of the lateral bronchi in the lungs of mammals, shows that they are disposed in two series with relation to the pulmonary artery. There is a series which is anterior to the artery at its entrance into the lung, and this is called the **epiarterial series of bronchi**, and the other series is posterior to it and is called the **hyparterial series** (HY.BRO). In the great majority of mammals the epiarterial series is much reduced, and is represented by a single lateral bronchus on either side, while in some, as in the rabbit for instance, it is still further reduced and is represented by a single bronchus on the right side only (Fig. 46, R.EPL.BRO), that on the left having disappeared.

Each lung of the rabbit is divided by fissures or clefts into **lobes**, of which there are two in the left and four in the right lung. If the relation of these to the epiarterial and hyparterial bronchi be examined, it is evident that the most anterior lobe (L.AN.L) of the left lung is not homologous to that (AN.AZ.L) of the right; for the anterior lobe of the left lung belongs to the first bronchus of the hyparterial series (HY.BRO), while that of the right belongs to the last of the epiarterial

series (R.EPL.BRO). And it is at once evident that it is the middle lobe of the right lung that is the homologue of the anterior lobe of the left; hence these are named respectively the **right anterior** (R.AN.L) and **left anterior** (L.AN.L) lobes. The anterior lobe of the right lung is called the **anterior azygos lobe** (AN.AZ.L) because it is not paired. The biggest lobe of either lung belongs to the main bronchus and is named respectively the **right** and **left posterior lobe** (R.POS.L & L.POS.L). To the inner side of the right posterior lobe there is another not represented on the left side; it belongs to a lateral hyparterial bronchus and is named the **posterior azygos lobe** (POS.AZ.L).

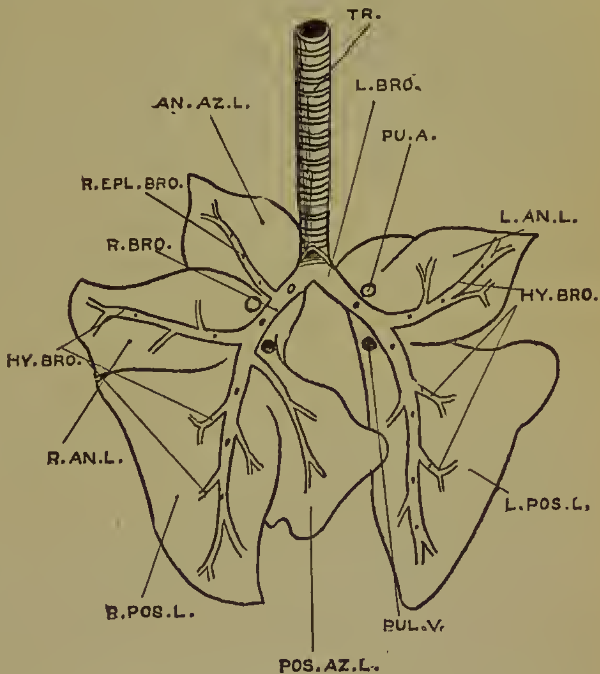


FIG. 46. Dissection of the lungs of the Rabbit (*Lepus*), to show the branching of the bronchi and their relation to the pulmonary artery. The pulmonary artery and vein are represented as cut across at the point where they enter the lung. AN.AZ.L = anterior azygos lobe; L.AN.L = left anterior lobe; L.BRO = left bronchus; L.POS.L = left posterior lobe; HY.BRO = hyparterial bronchi; POS.AZ.L = posterior azygos lobe; PU.A = pulmonary artery; PUL.V = pulmonary vein; R.AN.L = right anterior lobe; R.BRO = right bronchus; R.EPI.BRO = right epiarterial bronchus; R.POS.L = right posterior lobe; TR = trachea.

The **larynx** is the most anterior portion of the windpipe, and is composed of a stout band of cartilage bent in the form of a V, with the apex situated ventrally and the diverging limbs directed dorsally; this cartilage is the **thyroid**, the so-called 'Adam's apple' of man's larynx. Posterior to it, and situated partly within it, is a ring-like cartilage, the **cricoid**, which is so articulated with the thyroid that either is capable of turning, as upon a pivot, upon each other. Anteriorly to the thyroid, and lying just within the antero-dorsal horns of its divergent limbs, are a pair of triangular cartilages, the

arytenoids. The vocal cords are thickened folds of the membrane that passes on either side from the arytenoids to the ventral angle of the thyroid, and by the contractions of the various muscles that move the cartilages they may be rendered tense or lax, closely approximated or more widely separated. The **epiglottis** is a small cartilage lying just behind the root of the tongue and overlooking the glottis. It serves to deflect the food-stream from the middle line, so that it passes round and not over the breathing aperture (glottis). The **trachea** (TR) is attached to the posterior rim of the cricoid and passes down along the ventral surface of the cervical vertebral column to reach the thorax, where it divides into two bronchial tubes or **bronchi**, one for each lung. It is a membranous tube composed of fibrous and elastic tissue, and supported by a series of incomplete rings of cartilage, which serve to keep the lumen of the tube open when the neck is more or less bent in the course of the ordinary movements of the animal. Internally it is lined with ciliated columnar epithelium, the movements of the cilia of which are in such a direction that particles are carried from within to without. Opening on to the internal surface of the tube are a number of glands which are continually pouring out a sticky material called mucus, the principal function of which is to catch any foreign particles that may have gained access to the trachea; and as the mucus is continually moving towards the mouth by the action of the cilia, these are at the same time carried with it.

A comparison of the lung of the frog with that of the rabbit, when made in conjunction with a study of the development of that of the latter, shows that there is no fundamental distinction between the two, other than that the one represents a stage of organization in advance of the other. The lung of the frog is a mere membranous sac, that of the rabbit a similar sac, from which many diverticula have grown out. Embryologically the lung of the rabbit is like that of the frog, and it is only when there grows out from this primitive sac a number of other sacs (diverticula), and of others from these, that the distinctions which exist between them begin to arise. The membranous nature of the essential part of the lung of the rabbit is obscured because connective and elastic tissues have developed and fill up the spaces between the membranous sacs (diverticula or infundibuli); within this tissue the blood-vessels, capillaries, lymphatics, and nerves of the lung run and anastomose.

Even if this embryological evidence did not exist, we should have

arrived at the same conclusion with respect to the morphological nature of the mammalian lung, by the facts of comparative anatomy; for among the Amphibia and Reptilia there may be traced those morphological advances which the lung of the Mammalia exhibits as it passes through its successive stages of development. In other words, the ontogenetic history of the rabbit's lung repeats the phyllogenetic history of that organ as we trace it by the method of comparative anatomy.

CHAPTER VII

URINO-GENITAL SYSTEM

THE urino-genital system of Vertebrates consists of certain glandular **renal organs**, which are concerned in the extraction of nitrogenous waste from the blood, and of **generative** or **reproductive organs**, the business of which is the production of the male and female sexual elements and the means by which these may be brought together, as also those by which the young may be nourished and protected during their embryonic development. In early embryonic stages the gonads (reproductive glands) are not connected with the urinary organs; but as development proceeds, some of the renal ducts become wholly or partially converted into genital ducts.

Dogfish. The renal organs of the dogfish lie on either side of the dorsal aorta and outside the peritoneum. They consist in the adult of two portions, an elongated anterior part, the **mesonephros** (Figs. 47 & 48, MES), and a more compact, broader, and posterior portion, the **metanephros** (MET). Each part is composed of a series of tubules, called the **Wolffian** or **nephridial** tubules, bound together by connective tissue and in close relation to the capillaries of the blood-vessels supplying the kidneys. The mesonephros degenerates in the female, and does not form a well-defined tract, but occurs (Fig. 48, MES) in patches situated along either side of the vertebral column. In the male (Fig. 47) it is well developed and functionally active, and its duct, the **Wolffian** or **mesonephric duct** (Fig. 47, WO.D), is connected with the male sexual gland, the **testis** (TES), and is concerned with passing the sperm derived from that to the exterior, as well as carrying away the urinary products of the mesonephros. The duct runs a very sinuous course over the surface of the mesonephros,

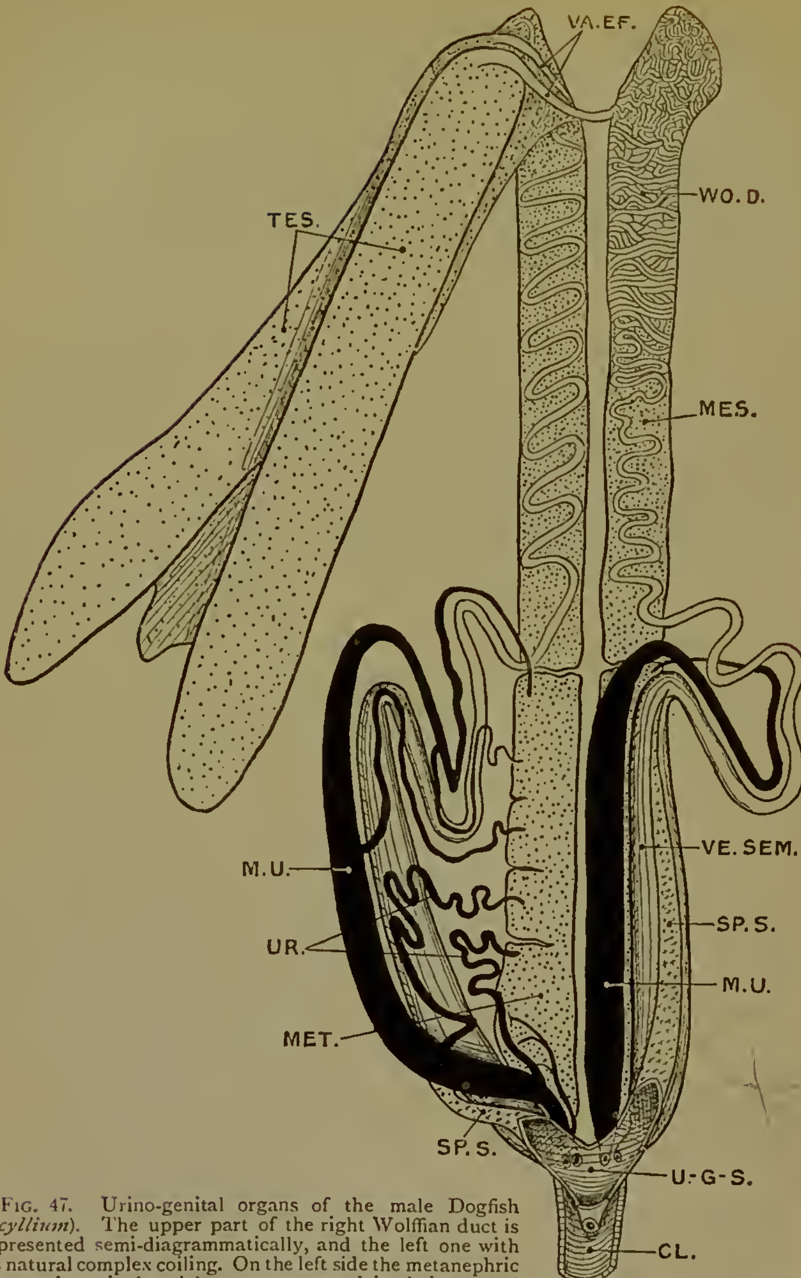


FIG. 47. Urino-genital organs of the male Dogfish (*Scyllium*). The upper part of the right Wolffian duct is represented semi-diagrammatically, and the left one with its natural complex coiling. On the left side the metanephric duct and seminal vesicle are represented in their natural relative positions, but on the right side they are pulled outwards so as to show the connexion between the duct and the metanephros by means of the smaller, lateral ducts UR. CL = cloaca; MES = mesonephros; MET = metanephros; M.U = main metanephric duct; SP.S = sperm sac; TES = testis; UR = lateral metanephric ducts; U-G-S = urino-genital sinus; VA.EF = vasa efferentia; VE.SEM = vesicula seminalis; WO.D = Wolffian (mesonephric) duct.

and posteriorly it enlarges considerably to form the **vesicula seminalis** (Fig. 47, VE.SEM), which opens by its hinder extremity into a thin-walled sac that lies on its ventral surface, called the **sperm sac** (SP.S). The latter is a tapering organ, ending blindly anteriorly, and posteriorly uniting with its fellow of the opposite side to form the **urino-genital sinus** (U-G-S), which opens into the cloaca (CL) upon its dorsal wall at the summit of a conical elevation, the **urino-genital papilla.** At its anterior end the mesonephros receives a number of very small tubes, the **vasa efferentia** (VA.EF), coming from the testis; these arise in the course of development as outgrowths of certain of the anterior Wolffian tubules, and thus through them open into the Wolffian duct, so that the latter acts partly as the excretory tube of the mesonephros and partly as a **vas deferens** (male genital duct) conveying the male cells (sperm) to the exterior.

In the female dogfish (Fig. 48, W.D) the Wolffian duct is very small, and runs a straight course over the surface of the mesonephros; posteriorly it enlarges to form a tubular **sac** (D.W.D), which, uniting with its fellow of the other side, forms the **urinary sinus** that opens into the cloaca behind the oviducts; it serves as an excretory tube only, and, unlike that in the male, has no connexion with the sexual gland.

The metanephros (MET) persists in both sexes as a functional renal organ, and is mainly composed of a number of renal tubules which are intimately related to the capillaries derived from the renal arteries and the renal-portal vein; the renal tubules open into four or five tubes, the lateral metanephric ducts (Fig. 48, MET.D & Fig. 47, UR), which leave the kidney along its outer border and in the male open into a large single tube called the **metanephric duct** or **ureter** (Fig. 47, M.U), and this enters the urino-genital sinus below the opening of the Wolffian duct. In the female (Fig. 48, MET.D) the metanephric ducts open separately into the urinary sinus.

The **reproductive organs** of the dogfish consist of a **sexual gland** or **gonad**, called the **testis** (TES) in the male and the **ovary** in the female (OVA), and of a tubular conducting channel which serves to convey the sexual products, **sperm** or **ova**, to the exterior, and which in parts is modified for the retention of these for a greater or longer period of time.

In the male (Fig. 47, TES) the gonad is paired, but the two testes are partially united. Anteriorly they each give off a series of small tubules, the **vasa efferentia** (VA.EF), which enter the mesonephros,

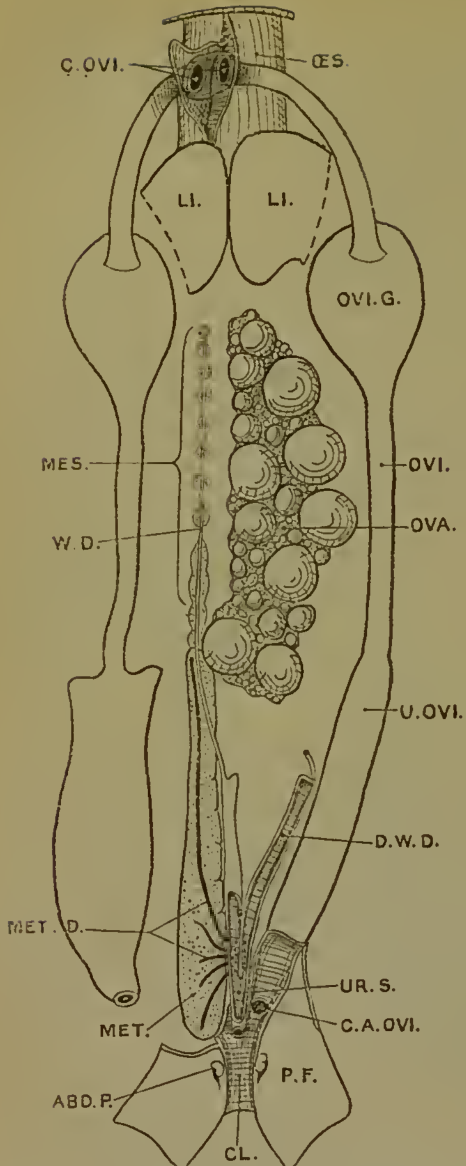


FIG. 48. Urino-genital organs of the female Dogfish (*Scyllium*). The right oviduct is represented with an egg-capsule in its lower portion; it has been cut away from the cloaca and displaced a little to the right in order to show the metanephros. The right renal organ is alone represented, and the Wolffian duct of the left one is represented only in its lower part. ABD.P = abdominal pore; C.A.OVI = cloacal aperture of oviduct; C.OVI = cœlomic aperture of oviduct; CL = cloaca; D.W.D = distal portion of Wolffian duct; LI = liver (anterior end); MES = mesonephros; MET = metanephros; MET.D = metanephric ducts; ŒS = œsophagus; OVA = ovary; OVI.G = oviducal gland; OVI = oviduct; P.F = pelvic fin (part only); UR.S = urinary sinus; U OVI = uterine portion of oviduct (that of the right one contains an egg-capsule); W.D = Wolffian (mesonephric) duct.

and the further course of which has already been described, as well as the course and relations of the **vas deferens (Wolffian duct)** (WO.D).

In the female (Fig. 48, OVA) the gonad (ovary) is single, but in other genera of dogfishes it is a paired organ. It has a tuberculated surface, due to the presence of ripening and matured ova, and it lies a little to the right side of the middle line of the body. It is not directly connected with the **oviduct** (OVI) or female sexual duct that conveys the eggs to the exterior, so that as the eggs are liberated from the surface of the ovary they fall into the body cavity (cœlom), and subsequently enter the internal or **cœlomic aperture** (C.OVI) of the oviducts by processes which are not yet known, but which are thought to be connected with the muscular movements of the body. The oviducts are paired tubular organs, opening into the body cavity usually by a common aper-

ture at the one end, and each by its own aperture (Fig. 48, C.A.OVI) into the cloaca, and thence to the exterior at the other. In some instances their cœlomic apertures, instead of being a common one, open independently into a membranous sac with a very widely open aperture: Fig. 48 was copied from such a case. At about the end of its anterior third the oviducal walls are very much thickened and glandular, forming a prominent globular swelling, the **oviducal gland** (OVI.G), which secretes the horny capsules of the eggs. Behind the gland the posterior third of the oviduct is very much enlarged (U.OVI), and is capable of considerable distension; the epithelium of its wall is longitudinally folded, and in certain dogfishes and other Elasmobranchs they give rise to glandular finger-like processes which fit into corresponding villi of the yolk-sac of the developing embryo, and by which means an interchange of nutritive, excretory, and respiratory products can take place between the fœtal and maternal blood. In such cases the young are retained in the uterine portion of the oviduct until they are fully formed, and at the time of their liberation they are capable of finding their own food and otherwise protecting themselves. But in the case of the more commonly occurring dogfish, *Scyllium canicula*, the young embryo, invested in a horny capsule, is liberated from the oviduct in an immature condition, and undergoes its further development while the egg-case is floating in the sea a little below the surface of the water. The horny capsule (egg-case) is produced at each of its four angles into a long spirally-twisted, tendril-like process, by means of which it may be attached to any floating object, and thus the aëration, by diffusion, of the blood circulating in the yolk-sac is facilitated.

The male dogfish possesses externally certain accessory sexual organs which are used in copulation. These are known as the **claspers** (Fig. 8, CL), and are formed as posterior and nearly median extensions of the pelvic fins; they are conical, rod-like bodies in form, one on each side of the middle line, and each is grooved along its inner-dorsal surface. In the act of sexual union these claspers are inserted in a closed condition (applied together) into the cloaca of the female, and thence one into either oviduct, when the seminal fluid passes along their grooves and is thus poured into the distended oviducts. The spermatozoa, which are very actively motile, must then move towards the anterior end of the oviduct, past the oviducal gland, when they meet the eggs which they fertilize. The aperture of the two oviducts into the cloaca is, in the virgin dogfish, closed by a thin membrane,

the hymen, the morphological and physiological significance of which is unknown. It is found in rays and sharks, but not in other fishes, and also in most mammals.

Frog. The renal organ (Figs. 49 & 50, ME) of the frog is a mesonephros [1], and consists of a pair of elliptical flat bodies, situated one on either side of the dorsal aorta in the posterior two-thirds of the body cavity. Each is composed of a large number of urinary (Wolffian) tubules, dilated at one end, and at the other opening into the Wolffian duct (WLF.DU). The dilated portion of each tubule, known as a **Malpighian capsule** (Fig. 95, D), contains a tuft of capillaries, called a **glomerulus** (G), derived from the renal arteries, while the tubular portion is lined along the greater part of its course by a glandular epithelium, and over its outer surface a dense meshwork of capillaries, derived from the renal-portal vein, freely anastomoses [2].

The Wolffian duct (WLF.DU), which in the male acts also as a vas deferens, extends along the outer border of the mesonephros or kidney, being embedded in the substance of the organ, and opens into the cloaca upon a minute papilla. In the male (Fig. 49), in correlation with its seminal function, its posterior portion is dilated into a large saccular organ, the **vesicula seminalis** (VE.SE). The Wolffian duct is therefore, in the male, a urino-genital one. The ventral surface of the kidney in the frog is beset with a large number of ciliated openings, called **nephrostomes**, which communicate at their internal terminations with the blood-vessels derived from the renal-portal vein. This connexion is peculiar and is secondarily acquired, for primitively the nephrostomes open into the uriniferous tubules, but subsequently lose this connexion and acquire that above mentioned. The kidneys lie in a large lymph space, and as the cilia of the nephrostomes are working in such a direction that currents from without to within are produced, it follows that a portion of the lymph is carried through them into the general blood circulation, *via* the renal veins; whereas in the larva, when they were connected with the uriniferous tubules, the lymph was simply passed to the exterior and lost.

The male reproductive organs consist of a pair of oval bodies, the **testes** (Fig. 49, TES), situated upon the ventral surface of the kidneys at their anterior ends. The **vasa efferentia** (VA.E) leave the testis

[1] See p. 190 on the 'Development of the Renal Organs.'
[2] See Renal-portal blood system.

from its inner surface and pass to the inner border of the kidney, where they open into a longitudinal tube, from which other tubes pass out transversely and pour their contents into the uriniferous tubules, which open directly into the Wolffian duct.

The female reproductive organs consist of a pair of **ovaries** (Fig. 50, OV) and two oviducts. The ovaries are situated on the ventral surface of the kidneys, in the same position as the testes in the male, and the size and appearance of which varics with age. In young frogs each ovary is a small yellow, and slightly tuberculated body, but in older frogs—those which have reached sexual maturity—it is much larger, and black in colour. It consists of a large number of eggs (ova) in various stages of maturity, embedded in a delicate stroma of connective tissue, the whole being limited by a thin membrane and further invested by the peritoneum. In the male and female, each gonad bears at its anterior end a much fimbriated fatty body, called the **corporum adiposum** (Fig. 49, COR.AD).

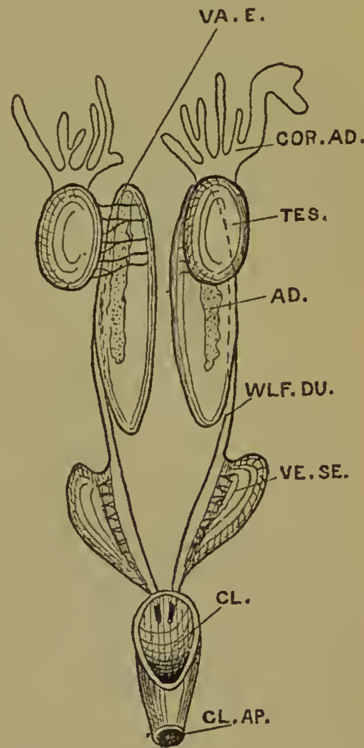


FIG. 49. Urino-genital organs of male Frog (*Rana*). AD = adrenal body; CL = cloaca; CL.AP = cloacal aperture; COR.AD = corpora adisposa; TES = testis; VA.E = vasa efferentia (the right testis has been turned to one side in order to show the VA.E); VE.SE = vesicula seminalis; WLF.DU = Wolffian duct.

The oviducts can be divided into thiee regions, an anterior thin-walled receptive portion, which opens to the body cavity by a funnel-like aperture just behind the root of either lung (CŒ.AP); a middle thick-walled glandular portion (GLA.P), which is much the longest of the three regions and secretes the albuminous investment for thc cgg; and a posterior dilatablc portion (UT.P), the walls of which contain unstriped muscle fibres, and which rctain the eggs until the period of their extrusion. Thc last part is known as the **uterine portion** of the oviducts, and is capable of very great distension; just prcvious to the cjection of the cggs they contain the wholc of the ripcned ones, with their albuminous coats, from the ovary. The

oviducts open into the cloaca just in front of the opening of the Wolffian ducts.

Fertilization of the eggs is external in the frog, unlike that in the dogfish and rabbit, where fertilization takes place in the upper portions of the oviducts. During the breeding season, extending from February to March or April, the frogs gather in large numbers along the banks of streams and ponds for the purpose of mating, during which process the male frog emits intermittent croaking sounds, produced by the vibration of the walls of the vocal sacs. It is possible that this not altogether discordant sound has to do with attracting the female frog, very much as the warbling of some songsters and the gay plumage of other male birds has to do with winning the affections or the vanities of the hen. It may be that the croak of one male frog is more pleasing to a particular female than that of any other male, and thereupon she accepts him as her mate. But whether this be so or not, the act of mating consists of the male frog embracing the female round the body just behind the arms; and for purposes of obtaining a firmer hold, the thumb of the male bears a large callosity or swelling which reaches its maximum development at the breeding period, and at the same time the biceps

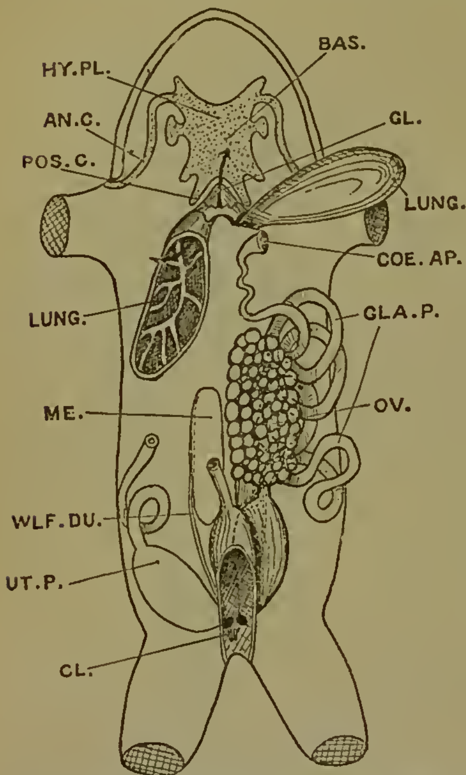


FIG. 50. Ventral dissection to show urino-genital organs of female Frog (*Rana*). The left lung has been reflexed forwards in order to show the cœlomic aperture of the oviduct, and the right one cut open in order to show its cavity. The distal portion only of the right oviduct has been represented, and the ventral wall of the colon has been cut away to show the apertures of the oviducts and mesonephric ducts upon its dorsal wall. The left ovary only is represented, and only the distal part of the right oviduct. AN.C = anterior cornu of hyoid plate; BAS = basihyal; CL = cloaca; CŒ.AP = cœlomic aperture of oviduct; GL = glottis; GLA.P = glandular portion of oviduct; HY.PL = hyoid plate; ME = mesonephros (kidney); OV = ovary; POS.C = posterior cornu; UT.P = uterine portion of oviduct; WLF.DU = Wolffian (mesonephric) duct.

muscle becomes much larger. They may remain in this condition of embrace for hours, days, or even weeks, until the female extrudes the eggs, which then become fertilized by the simultaneous outpouring of the seminal fluid from the male. Sexual union always takes place along the margin of water, so that the extruded eggs pass at once into it, when the albuminous envelope, by the imbibition of water, swells and forms a gelatinous coat. Within this gelatinous coat the spermatozoa bore their way towards the egg, which is ultimately entered by one of them, after which, by alteration in the vitelline membrane, other spermatozoa are prevented from entering.

Rabbit. The renal organs of the rabbit (Fig. 52, K) consist of two oval bodies situated one on either side of the vertebral column, the right-hand one a little in front of the left. The inner border of each **kidney** is deeply notched, forming the **hilus** (H), at which part the renal nerve and artery enter, and the vein and ureter leave it. Each kidney is invested in a tough connective tissue sheath, which can be easily stripped from it without injury. The renal substance is composed of an outer denser **cortical layer** (CX), enclosing an inner softer **medullary portion** (M), which towards the hilum is formed into a few projecting conical papillæ, the **pyramids** (PYR), the apices of which open into the enlarged cup-shaped dilations of the ureter just inside the hilus, and which are known as the **calyces** (CA).

The renal artery, upon entering the kidney, breaks up into a number of branches which pass between the pyramids to enter the deeper substance of the organ, and at the junction of the cortex and medulla they divide and form a series of arches, the **renal arterial arches**, from the outer and inner surfaces of which straight branches are given off. Those arising from the outer surface pass directly outwards towards the periphery of the cortex, giving off very small arterioles, the **afferent renal arteries**, which pass horizontally to the Malpighian capsules of the uriniferous tubules. The arteries arising from the inner surfaces of the arterial arches, the **vasa recta**, pass through the medullary portion of the kidney. The arrangement of the veins is very similar to that of the arteries.

The greater portion of the substance of the kidney is composed of microscopic tubes, the **urinary tubules**, which at the one end open into the calyces of the kidney, and at the other end terminate blindly in a dilated and invaginated sac, the **Malpighian capsule**, into which a tuft of blood capillaries, the **glomerulus**, derived from the afferent renal artery, is inserted. The urinary tube in the mammal

follows a definite and very complicated course, each change in which is marked by definite and constant histological characters. The first portion of the tube, i. e. that immediately following the Malpighian capsule, follows a wavy course, and is lined with columnar epithelium, the cells of which are usually more or less granular; this, the **convoluted tubule**, is followed by a long loop, the **loop of Henle**, the descending limb of which is lined with flattened epithelium, and is not, therefore, glandular in nature; the ascending limb is lined with an epithelium composed of polyhedral cells, and passes into a tube (**irregular tubule**) which runs an irregular course and is characterized by its angular bends, the epithelium lining it being composed of angular and imbricated cells. This portion of the tube is followed by a convoluted one (**distal convoluted tubule**), similar in every respect to that arising from the Malpighian capsule, and which ultimately opens into a **collecting tubule** that runs to the apex of one of the urinary pyramids, whence it discharges its contents into the pelvis of the ureter. The loop of Henle and the collecting tubule runs in a radial direction in the medullary portion of the kidney, while the two convoluted tubules, the irregular or zigzag tubule and the Malpighian capsule, are restricted to the cortical portion. The afferent renal artery enters the Malpighian capsule and breaks up into a tuft of capillaries, which ultimately converge and form a small vein, the efferent renal vein, which emerging from the capsule, once more breaks up into a second set of capillaries over the convoluted and irregular tubules. The veins derived from the union of this second set of capillaries enter the renal venous arches, and thence the blood is returned to the renal vein, which leaves the kidney at the hilus.

Sexual organs. The **testes** of the male are developed in the same position as the ovaries of the female, but at the period antecedent to sexual maturity they pass through a passage just in front of the anterior border of the pelvis, the **inguinal canal**, and pushing the peritoneum and body-wall in front of them, form two pendent pouches, called the **scrotal sacs**, which come to lie behind the penis. In some mammals, i. e. those in which the inguinal canal remains large, the animal can retract the testes and scrotal sacs within the body cavity, allowing them to descend at periods of sexual excitement. The testes are held in position in the scrotal sacs by a double membrane, the **mesorchium**, which is formed by the reflection of the peritoneum (tunica vaginalis) lining the sacs; at their posterior ends they are also held to the sacs by a short cord—the **gubernaculum**. Each

testis (Fig. 51, T) is an ovoidal body, bearing a prominence at either end, the anterior of which is called the **caput** (CA.EPD), and the posterior, the **cauda epididymis** (CAU.EPD); they are connected with each other by a tubular channel that passes along the inner border of the testis. The **vas deferens** (V.DE), or the duct which conveys the sperm to the exterior, leaves the testis at the cauda epididymis, and passes forward to reach the perineal cavity of the abdomen; thence turning round the ureter of the same side, it passes backwards and reaches the dorsal surface of the bladder, where it slightly dilates, and in contact with its fellow of the other side enters the ventral wall of a large sac, the **uterus masculinus** (UT. MA), which is situated between the bladder and rectum. The neck of the urinary bladder (U.BL) is prolonged backwards into a long canal, the **urethra** (URL.C),

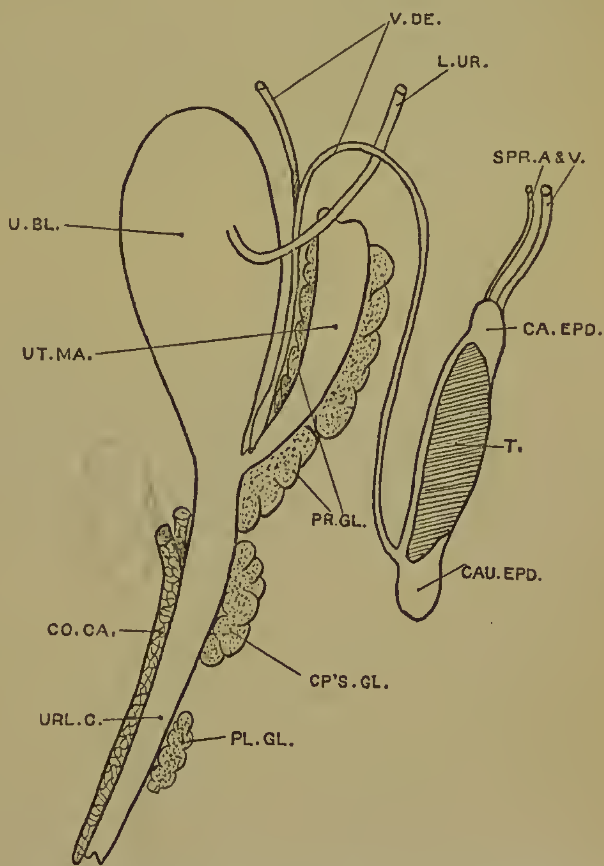


FIG. 51. Side view of the urino-genital organs of male Rabbit (*Lepus*). One testis only is represented. CA.EPD = caput epididymis; CAU.EPD = cauda epididymis; CO.CA = corpora cavernosa; CP'S.GL = Cowper's gland; L.UR = left ureter; PL.GL = perineal gland; PR.GL = prostate gland; SPR.A & V = spermatic artery and vein; T = testis; U.BL = urinary bladder; URL.C = urethral canal; UT.MA = uterus masculinus; V.DE = vas deferens.

that runs along the length of the penis and opens to the exterior at its apex. The uterus masculinus opens into this canal at its junction with the neck of the bladder, so that it plays the part of a **urino-genital**

canal, conveying the urinary products and seminal fluid to the exterior.

There are certain accessory glands whose secretions appear to be important in the formation of the seminal fluid, and which are known as the **prostate** (PR.GL) and **Cowper's glands** (CP'S.GL). The former consists of four or five lobes, i. e. a median anterior one situated on the dorsal surface of the uterus masculinus and bilobed in front; behind this a posterior lobe, sometimes divided into two; and two lateral lobes which lie between the vas deferens and the ventral wall of the uterus masculinus. They open independently into the urethral canal, and their secretion appears to play an important part in exciting the spermatozoa to activity. Cowper's glands are paired, and are situated on the dorsal wall of the urino-genital canal behind the prostatic glands.

The male copulatory organ or **penis** consists of two stiff, closely applied spongy rods, the **corpora cavernosa** (CO.CA), which lie along the ventral wall of the urethra, and are attached to the pelvic girdle posteriorly by two diverging portions, the **crura penis**. The dorsal wall of the penis is soft, yielding, and very vascular, and consists largely of a spongy tissue, the **corpus spongiosum**. The free extremity of the penis is terminated by a soft conical prolongation of the united corpora cavernosa, the **glans penis**, which projects beyond the loose skin, the **prepuce**, investing the extremity of the penis.

The female genital organs consist of a pair of gonads, the **ovaries** (Fig. 52, L.O), situated in the lumbar region, one on either side of the middle line, and studded over with small round pinkish projections, the **Graafian follicles** (OV), which contain the eggs or ova; and of a pair of **oviducts**, each of which is differentiated into three regions, i. e. a **Fallopian tube** (F.T), a **uterus** (L.UT), and a **vagina** (V). The free extremity of the Fallopian tube ends in a wide, membranous, funnel-shaped expansion with a fimbriated margin that more or less closely clasps the ovary; throughout the first part of its course it is narrow and slightly convoluted, but posteriorly it somewhat suddenly enlarges to form the **uterus**. The two uteri enter the anterior end of a wide tube, the **vagina** (V), on the summit of two conical elevations, by two apertures, the **os uteri**, which are capable of great distension. Between the two elevations, and projecting for some little way behind them, may be seen the **vaginal septum**; this is a vestigial structure, and is the last indication of the primitively

paired nature of the vagina and its origin by the confluence of the two oviducts in this region, the inner walls of which became absorbed,

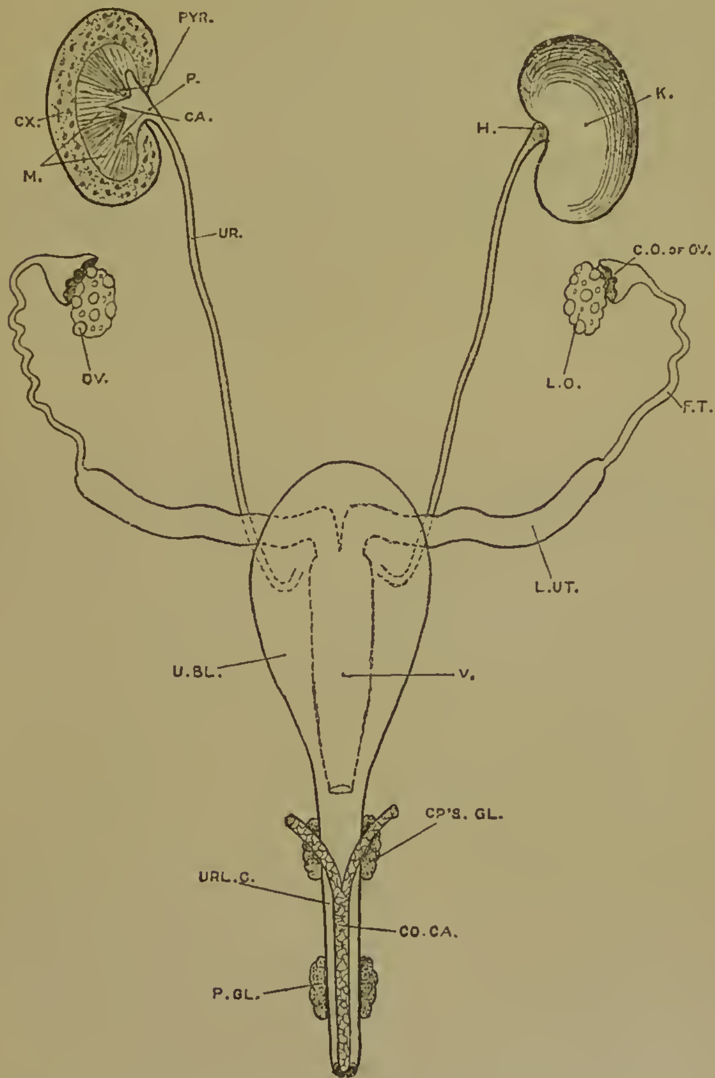


FIG. 52. Ventral view of the urino-genital organs of the female Rabbit (*Lepus*). The right kidney has been bisected in the median plane in order to reveal its gross structure. CA = calyce; CO.CA = corpora cavernosa; CO. of OV = cœlomic aperture of oviduct; CP'S.GL = Cowper's gland; CX = cortex of kidney; F.T = Fallopian tube; H = hilum of kidney; K = kidney; L.O = left ovary; L.UT = left uterus; M = medulla of kidney; OV = Graafian follicles containing ova; P = pelvis of ureter; P.GL = perineal gland; PYR = pyramid of kidney; U.BL = urinary bladder; URL.C = urethral canal; UR = ureter; V = vagina. The small black dots in the cortex of the kidney represent the glomeruli.

all but that part represented by the septum. The vagina enters the urethral canal (URL.C) by an aperture which occupies the same relative position as that of the uterus masculinus in the male. The ventral wall of the urethral canal is stiffened by two corpora cavernosa (CO.CA), as in the male, but they are not so strongly developed; they are united along the greater part of their length, and the free extremity projects slightly beyond the **vulva** or aperture of the urethral canal as a **clitoris**.

Cowper's glands are very much reduced in the female, and not infrequently are absent altogether. The prostate gland is never present.

In both sexes, near the free end of the urethral canal, there is a pair of scent-glands, called the **perineal glands** (P.GL), which pour their semi-fluid secretion into two hairless **perineal spaces**, one on either side of, and just anterior to, the aperture of the rectum.

Development of the Urino-genital Organs.

As with all the other organs of the body, an intelligent conception of the nature of the correspondence between the same organs in different animals is only possible with a knowledge of their development.

The renal organ of the dogfish, in the earliest period of its development, consists of three pairs of convoluted tubules, metamerically arranged, lying in the head region, on either side of the body; each tubule opens to the cœlom by a ciliated funnel-like aperture, called a **nephrostome**, which lies in close relation to a vascular tuft-like outgrowth of the aorta, called a **glomerulus**. This organ is called the **pronephros**, and is the functional renal organ of the young dogfish; the tubules of which it is composed open at one end into the body cavity, and at the other into a paired longitudinal tube, which apparently arises from the epiblastic germinal layer, and that runs nearly the whole length of the body, opening posteriorly into the cloaca. At this stage these tubes are called the **pronephric ducts**.

A little later, another set of tubules, called the **mesonephric tubules**, arise behind the pronephros, and which from their beginning open at their inner extremities into the cœlom in close approximation to glomeruli; but not until later do their other extremities acquire an opening into a duct which arises by the splitting of the pronephric duct into two. Of the two ducts which thus arise by the splitting of

a primitively single one, that into which the second set of tubules open is called the **Wolffian** or **mesonephric duct**, and that which remains connected with the pronephros is known as the **Müllerian duct**. The second set of tubules, situated in the anterior half of the trunk, is called the **mesonephros**, and it replaces the pronephros as a functional renal organ, which in the dogfish ultimately disappears.

Shortly after the mesonephros has appeared, a third set of tubules are developed immediately behind it, and which arise, apparently, as a posterior extension of it; they do not, however, open into the Wolffian duct, but into a series of others, independently acquired, and which are called **metanephric ducts** or **ureters**. This third set of tubules is usually called a **metanephros**, but as to how far it really corresponds to the metanephros of the rabbit, or as to whether it is only a posterior extension of the mesonephros, is a matter not yet settled beyond doubt. The metanephric tubules of the rabbit arise as outgrowths of the ureter (metanephric duct), whereas those of the dogfish arise *in situ* in the mesoblast, and become secondarily connected with their respective ducts; in other words, the mode of development of the so-called metanephros of the dogfish is very similar to that of its mesonephros.

All the organs mentioned above are developed in male and female alike, but their ultimate fate differs in the two sexes, some progressing while others retrogress.

In the female, the anterior ends of the Müllerian ducts grow forward and become confluent in the middle line, and open to the cœlom by a common aperture; they enlarge very much, undergo other changes, and ultimately become the oviducts. The Wolffian duct does not develop greatly, and the mesonephros, with which it is connected, undergoes partial retrogression, and is largely converted into lymphoidal tissue. The metanephros becomes the definitive kidney, and the metanephric ducts persist as the ureters.

In the male dogfish the Müllerian duct atrophies. The Wolffian duct becomes connected anteriorly, through the Wolffian tubules, with the vasa efferentia of the testis. The secondary connexion between the testis and the Wolffian duct is brought about in the following way: from some of the anterior Wolffian (mesonephric) tubules, tubular outgrowths arise and grow forward towards the testis, with which they become permanently connected. These tubular outgrowths form the vasa efferentia. Posteriorly the Wolffian duct enlarges to form the seminal vesicle, from which the sperm-sac arises as an outgrowth.

The mesonephros persists as a functional kidney, and pours its products into the Wolffian duct, which thus becomes a urino-genital duct, as in the male frog. The metanephros and its ducts become the definitive kidney and ureters.

In both sexes the pronephros disappears, as in the majority of cases, though it persists in a functional condition throughout life in a few fishes.

In the **Frog** the series of changes just described are very much the same, but the metanephros and metanephric ducts are never developed, so that the definitive kidney is a mesonephros; and the pronephric duct does not split into two, but becomes the Wolffian duct, the Müllerian duct probably arising in great part independently of it from a modified tract of cœlomic epithelium. The Müllerian ducts become the oviducts in the female, and may be found in most male frogs, but in an embryonic condition; and in some they disappear altogether. The Wolffian ducts become the mesonephric ducts (ureters) in the female, and the urino-genital ducts in the male.

In the **Rabbit** the pronephros is never formed; the mesonephros is very large, and is connected with the Wolffian duct, which arises, *sui generis*, from the mesoblast layer, and not from the splitting of an antecedent duct, as in the dogfish, or from the pronephric duct, as in the frog; though it is probable that, phyllogenetically, the Wolffian duct of the rabbit is homologous with that of the frog. The Müllerian duct arises in a manner not yet clearly ascertained. The metanephric duct or ureter arises as a diverticulum of the Wolffian duct just before that enters the cloaca, and growing forward, its anterior end dilates and gives rise to branching tubular processes, which eventually become the uriniferous tubules of the metanephros or definitive kidney.

The mesonephros, judged by its size and vascular supply, is an important organ in the embryo; but the greater portion of it disappears in both sexes, a small part remaining as the parovaria (small cæcal tubules situated on the inner border of the ovary) in the female, while tubular outgrowths from some of its anterior tubules penetrate the testes of the male and ultimately form the vasa efferentia, which are a series of microscopic tubules, placing the epididymes in connexion with the tubules of the testes. The anterior portion of the mesonephros or Wolffian body becomes converted into the caput epididymis; while the proximal portion of the Wolffian or mesonephric duct gives rise to the cauda epididymis, and its distal portion to the vas deferens. In the female, the Wolffian ducts as a rule disappear, or else remain as merely vestigial structures known as Gärtner's ducts.

The Müllerian ducts, in the male, disappear, though it is possible that their distal portions give rise to the uterus masculinus. In the female they become greatly enlarged, and give rise to the Fallopian tubes, the uteri, and by confluence of their distal ends, with resorption of the coalesced walls, to the unpaired vagina.

The Origin and Ultimate Fate of the Parts of the Urino-Genital System, Tabulated.

		Dogfish.	Frog.	Rabbit.
Pronephros.	Male and Female.	Develops and is functionally active in the embryo, but disappears in the adult.	Develops and reaches a great size in the larval tadpole, but disappears in the adult.	Never develops.
Pronephric duct.	Male and Female.	Arises from the epiblast, and later splits into two, forming the Wolffian and Müllerian ducts.	Arises from the mesoblast, and after degeneration of the pronephros becomes the Wolffian duct.	Not represented as such.
Mesonephros (Wolffian body).	Male and Female.	Consists of an anterior and posterior portion. In the female the former degenerates, and in the male its anterior part becomes connected by vasa efferentia with the testis, and permanently functions as a renal organ: in both sexes the latter portion functions as the permanent kidney (so-called metanephros).	Consists only of one portion, and becomes the definitive (permanent) kidney of the adult. Some of the Wolffian tubules in the male produce tubular outgrowths which become (as in the dogfish) the vasa efferentia.	Is large and important in the embryo, but becomes much reduced in the adult and practically disappears. In the female it is represented by the parovaria. In the male, it gives rise to the vasa efferentia and to the caput epididymis.
Mesonephric (Wolffian) duct.	Female.	Does not progress much beyond the embryonic stage, and functions as the urinary duct of the mesonephros.	Becomes the urinary duct of the mesonephros.	Disappears altogether or remains as a vestigial body (Gartner's duct).
	Male.	Becomes much enlarged and forms a urino-genital duct; posteriorly by enlargement it forms the seminal vesicle.	Becomes a urino-genital duct, with a posterior enlargement or seminal vesicle.	Gives rise to the cauda epididymis and to the vas deferens.

		Dogfish.	Frog.	Rabbit.
Müllerian duct.	Female.	Becomes the oviducts. Arises by longitudinal division of the pronephric duct.	Arises independently of the Wolffian duct and becomes the oviducts.	Origin uncertain. Becomes the Fallopian tubes, uteri and vagina (oviducts).
	Male.	Degenerates.	Degenerates or remains in rudimentary condition.	Probably gives rise to the uterus masculinus.
Metanephros and Ureter.	Male and Female.	Probably unrepresented.	Does not develop.	The ureter arises as a diverticulum of the posterior end of the Wolffian duct, and the uriniferous tubules as diverticula of it. It becomes the definitive kidney.

CHAPTER VIII

THE TEGUMENTAL ORGANS

THE outer skin is derived from the epiblastic germinal layer, which is the layer that gives origin to the nervous system and the sense organs. It is composed of a superficial **epidermis**, into which blood-vessels do not penetrate, and a deeper **dermis**, originating from the mesoblast, in which the vascular channels and the nerves with the sense organs connected with them run. Various glands open upon the surface of the skin, which may arise from the metamorphosis of single cells (goblet cells) as in fishes, or may be simple chambers lined by flattened cells as in the frog, or more complex tubular organs as in the rabbit.

The skin in all animals is a protective layer, the efficiency of which is increased by the formation within it of bony scales, as in fishes and reptiles; it is also a sensory layer, placing the animal in conscious relation to its varying external conditions. In the frog and rabbit it performs the functions of an excretory organ by means of the sweat-glands developed in its substance, and in the former animal it is also respiratory in nature, allowing carbon dioxide to pass outwards and oxygen inwards.

Dogfish. The **mucous canals** (Figs. 25 and 36) which open upon the surface of the skin in the region of the head and which are particularly numerous upon the snout, contain a gelatinous material. The canals are sense organs, and each tube contains a little swelling of its wall, called an **ampulla**, which consists of modified epithelial cells, and with which the terminations of nerve fibres are connected. The surface of the skin is protected by imbricating scales, which are larger on the dorsal than the ventral surface, and the form of which varies slightly in different parts. As a rule, each scale consists of a four-lobed base from which a bony spine projects backwards at about an angle of 60°; the greater portion of the scale is composed of dentine, but the backwardly directed spine is capped with a layer of dense enamel. In the embryo dogfish the scales are covered by the epidermal layer of the skin, from which the enamel is developed, but the dentine of the spine and the bone of the base are developed from the mesoblastic layer of the dermis.

The scales of fishes are of two kinds: those whose margins are entire and which contain no enamel, the **cycloid scale**; and those in which the margin is serrated or denticulated, and in which the projecting spine is capped with a layer of enamel, the **ctenoid scale**, as in the dogfish.

The epidermis consists of several layers of cells, the deeper of which are composed of polygonal cells and the more superficial of flattened ones. The dermis is mainly composed of connective tissue with blood-vessels and nerves.

Frog. The skin of the frog is characterized by the absence of an exoskeleton of scales such as the dogfish possesses, a structural difference that is correlated with the additional function of respiration possessed by the frog's skin. Externally the **epidermis** of the skin is limited by a single layer of flattened cells, called the horny layer, and beneath this are several layers of cells, the outer ones of which are composed of more or less polygonal cells, and the deepest layer of all of columnar cells.

The **dermis** is composed of three layers of connective tissue, the most superficial of which (that which is attached to the epidermis) is a loosely meshed, much pigmented layer, and contains the **sweat-glands**. The middle layer is firmer and more compact, and is mainly composed of bundles of connective tissue running a horizontal course. At intervals, small bundles of fibres traverse the middle layer in a vertical direction and pass outwards into the superficial layer

between the glands. The deepest layer contains yellow elastic fibres as well as white fibres, and abundant blood-vessels and nerves.

The colour of the skin of the frog can vary from time to time with the varying external conditions. It is much lighter in colour on the ventral than the dorsal surface. The colour is due to branched connective tissue cells, called **pigment cells**, which are laden with pigment granules. The pigment cells occur partly in the epidermis, but are more numerous at the boundary between epidermis and dermis. It has been shown that these cells are influenced by stimulation of the nerves supplying the region of the skin in which they occur, and a structural connexion between one of the processes of the cells and nerve fibres has been made out.

The **sweat-glands** are globular sacs situated in the superficial layer of the dermis and opening to the exterior by a narrow conical canal; they are of two kinds, **serous** and **mucous**, the structure of both being similar. Their wall is composed of three layers, an outer connective tissue, a middle muscular, and an inner epithelial.

Rabbit. The skin of the rabbit is clothed all over with **hairs**, except at the hairless groove which divides the upper lip in the middle line and the perineal spaces on either side of the urino-genital aperture.

The **epidermis** consists of many layers of cells, the outermost of which are dead cells, which have undergone chemical and physical changes, and have become converted into horny scales; this layer is called the **stratum corneum**. The **stratum lucidum** consists of a layer of squamous cells closely arranged; beneath this is the **stratum granulosum**, composed of flattened cells containing granules and thicker in the middle than at the margins, so that they appear of a fusiform shape in sections. The **stratum Malpighii** is the thickest of the four layers, and its innermost layer of cells is columnar, while the cells of the outer layers are polyhedral in form. The cells of the deepest layer are continually dividing and thus form new cells, which passing gradually towards the surface, replace those lost by attrition and casting off at the horny layer.

The **dermis** is highly elastic and is composed of bundles of white fibrous and elastic tissues, interwoven in all directions, and forming numerous spaces or areolæ, which in the deeper portions of the dermis contain more or less fat; plain muscular fibres are also present. The outer surface of the dermis is raised up into little finger-like

elevations or **papillæ**, which contain either sensory end-organs or arterial loops.

The **glands** of the skin are of two kinds: **sweat-glands** and **sebaceous glands.**

The sweat-glands consist of a tube which runs a slightly spiral course from the surface of the epidermis through the greater thickness of the dermis, in the deeper part of which it becomes much coiled, forming a lobular mass embedded in the subcutaneous connective tissue and surrounded by blood-vessels. The wall of the gland is lined by columnar epithelium continuous with the epidermis, so that the gland is a tubular invagination of the epidermis. The sebaceous glands are minutely lobulated solid organs, the cells of which undergo retrogressive changes and give rise to a semi-solid oily substance; they mainly open into the hair follicles.

The **hair follicles** are pit-like invaginations of the epidermis, more particularly of the Malpighian layer, from the proliferation of the cells of which the hairs first take their origin.

The hairs are cylindrical in form, and arise fromt he hair papillæ at the bottom of the hair follicles. Each hair consists of a central **medulla**, an investing **cortex** and an outer **cuticle**. The colour of the hair is due to the pigment in the cortical cells, to the air contained in the spaces between the loosely arranged cells of the medulla, and in part to the degree of coarseness or fineness of the cuticular surface.

CHAPTER IX

THE MORPHOLOGY OF AMPHIOXUS LANCEOLATUS

(Lancelet)

Amphioxus lanceolatus (Fig. 53), as its specific name indicates, is a flattened lance-shaped animal; it is also pointed at both ends, a fact to which it owes its generic name. It is an organism that has suffered several changes in respect of its systematic position in the animal kingdom, for when first discovered in 1778 it was regarded as a species of slug and placed among the mollusca, under the name of *Limax lanceolatus*. Sixty years later it was discovered for the second time in the Mediterranean, and was regarded by Gabriel Costa as a kind of fish with affinities to the lampreys and hag-fishes. Costa

named it *Branchiostoma lubricum*, because he thought that the tentacle-like processes (Fig. 53, B.C) protruded round the mouth were

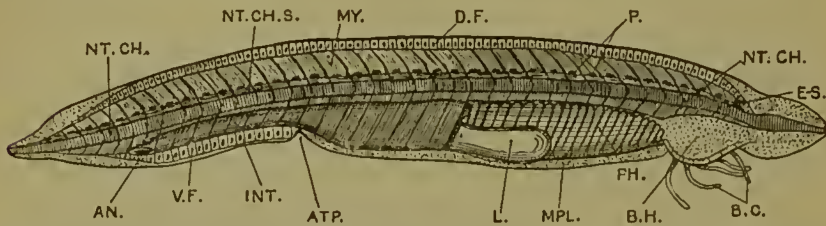


FIG. 53. A young specimen of *Amphioxus lanceolatus*, stained with borax carmine and clarified (rendered transparent) with oil of cloves, and drawn under the two-thirds objective of the microscope. The treatment renders it possible to see, without dissection, most of the internal organs. In the pharyngeal region, for about a third of the body length behind the buccal hood B.H, the body wall has been represented as being removed. AN = anus; ATP = atriopore; B.C = buccal cirri; B.H = buccal hood; D.F = dorsal fin; E-S = eye-spot; INT = intestine; L = hepatic diverticulum (liver); MPL = metapleural fold; MY = myotome (the number of myotomes are not correctly represented; they should be about twice as numerous); NT.CH = notochord; NT.CH.S = notochordal sheath. Immediately above this is a line of black dots P; these represent the pigment masses found along the length of the spinal cord. PH = pharynx; V.F = ventral fin.

respiratory in nature, and because of its remarkable dexterity in slipping through an observer's fingers. It was first named *Amphioxus* in 1836, in the *History of British Fishes*, written by William Yarrell.

It is a marine organism with somewhat degenerate habits that have reacted to a certain degree upon its organization. Its skeleton is exceedingly simple, consisting alone of a fibrous rod (Fig. 53, NT.CH) extending the whole length of the body, and in virtue of which in conjunction with the segmented arrangement of its muscles, it is enabled to burrow head foremost, with remarkable lightning-like rapidity, into the sandy bottom of the seas in which it lives.

During the whole of its larval life it is a free-swimming, active organism, but at adolescence it assumes a degenerate habit, burrows into the sand and remains covered by it, except for the anterior end containing the mouth, which just projects beyond the surface. Thus embedded it spends the remainder of its life, accepting whatever food, mainly in the form of minute vegetable organisms such as diatoms and desmids, that the currents of the water, set going by the action of the cilia along its pharynx, may bring to it. Occasionally it will leave its burrow and swim about for a short time, and then sink once more to the sandy bottom, where it will recline upon its side; under these conditions it is incapable of maintaining its equilibrium like an ordinary fish, but always topples over upon its side.

It has a world-wide but often arbitrary distribution, and prefers shallow to deep water. It is found in Plymouth Sound, in the English Channel, along the coast of France, upon the Atlantic and Pacific coasts of North and South America, and upon the shores of Australia, Japan, Ceylon, and Sweden. It is extremely abundant in the Gulf of Naples and along the north-eastern corner of Sicily.

External Form. The two extremities of the body are pointed, the posterior to a more marked degree than the anterior (Fig. 53). There is a membranous ridge, the **dorsal fin** (D.F), running along the mid-dorsal surface of the body, which becomes continuous with the more strongly developed **caudal fin**, at the hinder extremity of the body. Along the anterior two-thirds of the ventral surface there are two similar but larger ridges, the **metapleural folds** or **lateral fins** (MPL), which unite behind to form a single ventral median fold, the **ventral fin** (V.F), that extends backwards and becomes continuous with the caudal fin.

The **atriopore** (ATP) is an opening in the body-wall just anterior to the point where the two metapleural folds unite, and serves to place a cavity, the **atrial chamber**, that surrounds the pharynx (PH), in communication with the exterior. The **anus** (AN) is a small aperture, situated immediately to the left side of the ventral fin at the point where that becomes continuous with the caudal fin; it lies in the fifty-second **myotome** (MY) or **muscle-segment** of the body.

The mouth is situated at the anterior end of the body upon the ventral surface, and is guarded upon either side by a hood-like down-growth of the integument, the **buccal** or **oral hood** (B.H), supported along its free ventral margin by the cartilaginous **oral hoop** from which project the **buccal cirri** (B.C).

The oral hoop (Fig. 54, A & B, O.H) is a ring-like bar of cartilage, made up of a number of distinct pieces arranged end to end; from the end of each piece a ventrally directed process (B.C), the skeleton of the buccal cirrus, projects downwards.

The epithelium of the buccal cirri contains groups of sense cells, some of which contain a single vibratile cilium and others stiff hairs. Upon the inner surface of the oral hood, immediately in front of the real mouth opening, is a peculiar tract of sensory epithelium, drawn out into finger-like ridges. The cells of which it is composed are ciliated, and the action of the cilia is such as to cause a flow of water towards the mouth into the pharynx. It is called the rāderorgan.

The real mouth opening lies at the back of the vestibule formed by the oral hood, and is guarded by a circular membrane, the **velum**,

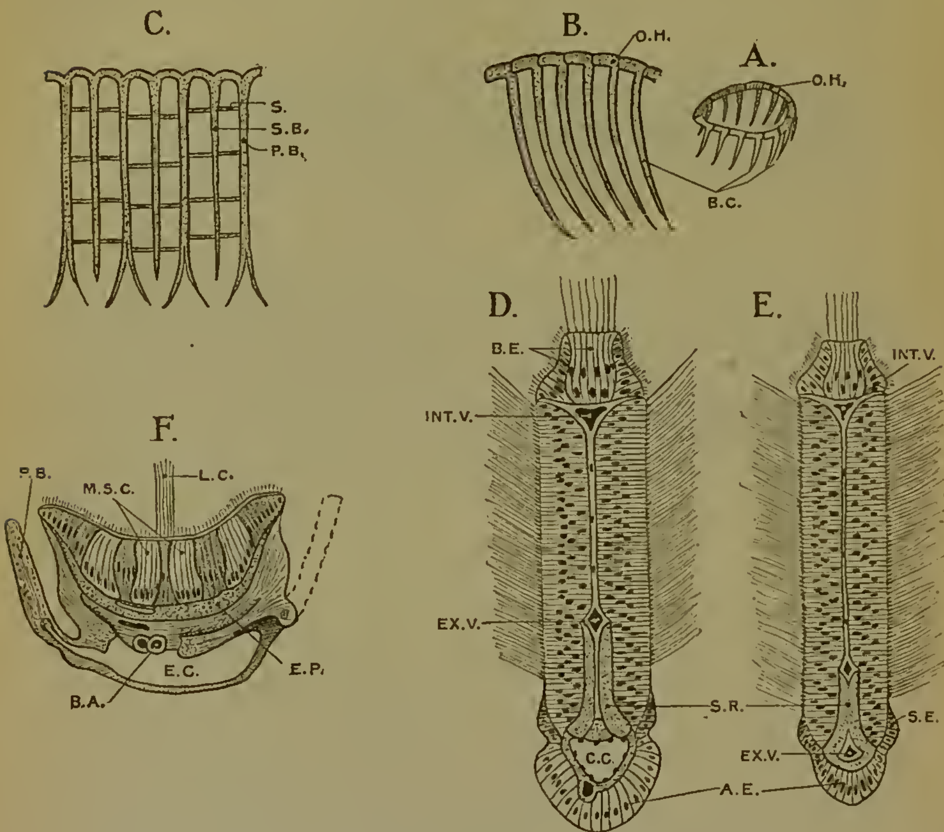


FIG. 54. A. Oral hoop of *Amphioxus*. B. Portion of A on a larger scale. C. Part of the pharyngeal wall cleaned of its epithelium to show pharyngeal bars. E. Transverse section of tongue-bar. D. Transverse section of primary bar. F. Transverse section of endostyle. E, D, and F are represented as seen under the one-sixth objective of the microscope. E, D after Benham, and F after Lankester and Willey. A.E = atrial epithelium of gill-bars; B.A = branchial artery; B.C = buccal cirri; B.E = branchial epithelium; C.C = cœlomic canal of primary bar; E.C = endostylar cœlom; E.P = endostylar plate; EX.V = external blood-vessel; INT.V = internal blood-vessel; L.C = long cilia of endostyle; M.S.C = mucous-secreting cells of endostyle; O.H = oral hoop; P.B = primary bar; S = synapticulæ; S.E = sensory (pigmented) epithelium; S.R = skeletal rod; S.B = secondary bar. The cœlomic blood-vessel of primary bar is not lettered, but is represented as a large black spot just outside the cœlomic canal C.C.

the margins of which are prolonged into twelve tentacular processes, the **velar tentacles**, which by crossing one another at the oral orifice form an efficient filter. The margin of the velum and the surface of the tentacles contain groups of sensory cells similar to those found upon the buccal cirri.

The mouth opens behind into the **pharynx** (Fig. 53, PH), which is perforated on either side by a large number of gill-slits, the walls of which are very thin and do not bear gill-filaments, like those of the dogfish and all other aquatic Vertebrates. In respect of the absence of the gill-filaments, the pharynx of *Amphioxus* resembles that of the Invertebrate *Balanoglossus*, although wide differences otherwise distinguish them.

The pharyngeal wall may be perforated by as many as a hundred and eighty clefts, on either side of which half this number are primary (Fig. 54, P.B); the other half (S.B) arise secondarily, and the bars which support them are not represented in other gill-bearing Vertebrates, unless it be by the thymus gland (see thymus gland, chap. vi).

Up to the later larval period, the gill-slits of *Amphioxus* are somewhat oval in form, with their long axes directed in the long axis of the animal; but after this a downwardly projecting portion of their dorsal wall divides the primitively single gill-slit into two, so that in the adult pharynx we may distinguish two sorts of bars arranged alternately, viz. **primary** (Fig. 54, P.B) and **tongue** or **secondary bars** (S.B).

Viewed from the side (Fig. 54, C) the pharyngeal slits are seen to be bounded by rod-like bars of chitinous material, dorsally supported by the notochord and ventrally attached in the middle line by means of the endostylar plates to the **endostyle** (Fig. 54, F, E.P), a median ridge extending along the floor of the pharynx (Fig. 55, END). Of these bars some are forked at their lower extremities, and the others end simply; the former are the **primary bars** and alternate with the latter, which are the **tongue** or **secondary bars**. Dorsally the two kinds of bars arch over one into another, and along their length are further strengthened by cross connexions, the **synapticulæ** (Fig. 54, C, S). Along the greater portion of the pharynx the gill-slits extend the width of its wall, but anteriorly and posteriorly they are much narrowed (Fig. 53).

The structure of the individual bars is best determined in transverse sections (Fig. 54, D, E, and Fig. 55, P & T), when it can be seen that the two kinds of bars are essentially the same, though they differ in certain important details. The skeletal rod of the primary bar (Fig. 54, D, S.R) is composed of a chitinous material and is somewhat lamellar in form; at its atrial surface (A.E) it is much expanded and encloses a tubular canal (C.C), that is continuous with the **dorsal cœlomic canal** (Fig. 55, D.CŒL.C) and which is, therefore, lined with

cœlomic epithelium (the nuclei of the epithelium is represented in the figures by dots). Stretching inwards from the bar is a septal membrane (Fig. 54, D) which affords a basis for the support of a columnar epithelium that covers it upon both surfaces; this epithelium is ciliated, except at the atrial end (A.E), where the cells are pigmented (S.E). The visceral (inner) edge (B.E) of the bar is covered by a columnar epithelium (branchial epithelium) arranged in three groups: a middle one, the cells of which possess very long cilia, and two lateral ones with very short cilia. The atrial (outer) end (A.E) of the bar is covered with a columnar epithelium (atrial epithelium) which is devoid of cilia.

The portion of the skeletal bar which encloses the cœlomic canal (C.C) is traversed throughout its length by a vessel, the **skeletal** or **cœlomic blood-vessel** (represented but not lettered in the figure), which arises from the **branchial artery** (Figs. 54 & 55, B.A), and after passing through the skeletal rod enters the **dorsal aorta** (Fig. 55, D.A) of the same side of the body. At the point of origin of the septal membrane from the skeletal rod, another blood-vessel, the **somatic** or **external vessel** (Fig. 54, D, EX.V), traverses the length of the bar; and at the inner edge of the septal membrane there is another, the **visceral** or **internal vessel** (INT.V). All these vessels are branches from a short bulb-like dilation of the branchial artery, and they all enter the dorsal aorta on the same side of the body as that of the pharyngeal bar through which they run.

The tongue or secondary bar (Fig. 54, E) is smaller in section than the primary, and the skeletal rod (S.R) is relatively smaller and simpler. There is no cœlomic canal unless, as may probably be the case, the channel through which the external blood-vessel (EX.V) runs is a cœlomic one. There is a difference of opinion among investigators as to this and the number of blood-vessels present in the secondary bar. Benham, to whom we owe our knowledge of the detailed structure of the pharyngeal bars, holds that the secondary as well as the primary bars contain three blood-vessels, such as are represented in our illustration, which has been copied from Benham's paper in the *Quarterly Journal of Microscopical Science.* But in the absence of further evidence it is preferable to adopt the conclusion of Willey and others, and to regard the cœlomic blood-vessel of the primary bars as being absent in the tongue-bars. In other respects the two bars are similar.

The **endostyle** has already been mentioned as a median ventral

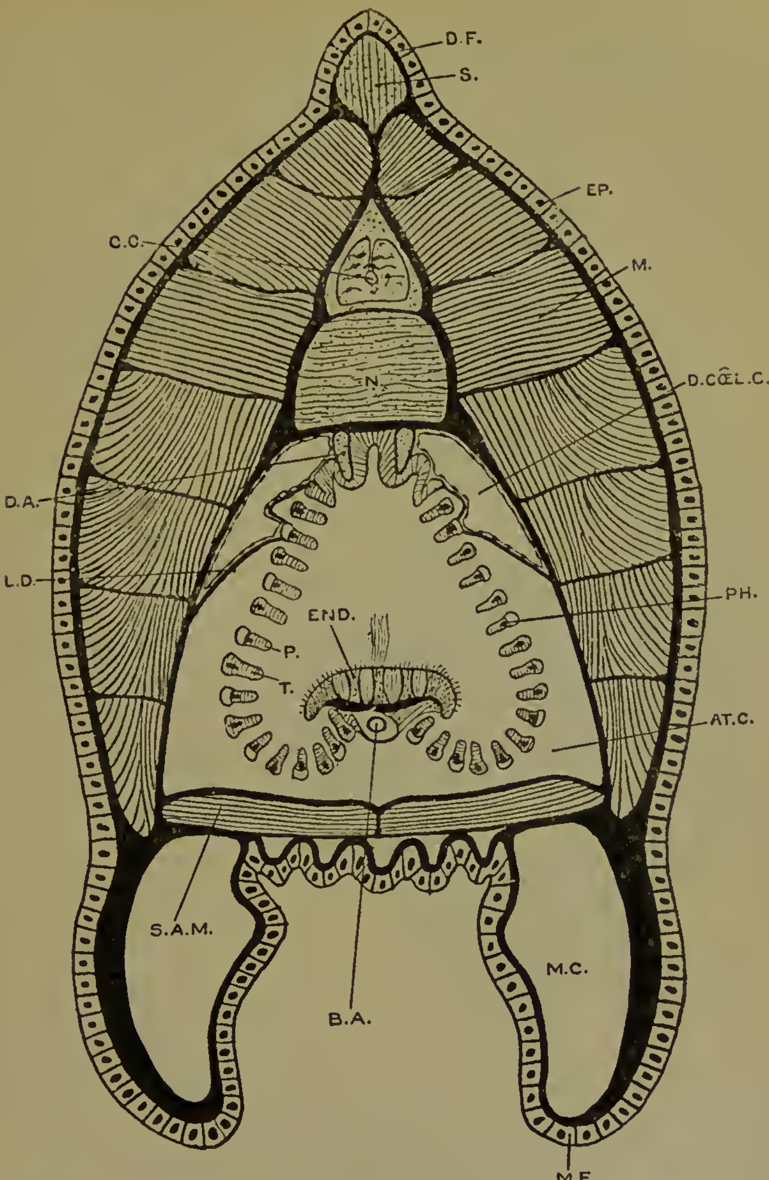


FIG. 55. Transverse section through anterior third of the pharyngeal region of *Amphioxus lanceolatus*. AT.C = atrial cavity; B.A = branchial artery; C.C = central canal; D.A = dorsal aorta; D.CŒL.C = dorsal cœlomic canal; D.F = dorsal fin; EP = epidermis; END = endostyle (hypo-pharyngeal groove); L.D = ligamentum denticulatum; M = muscle myomeres; M.C = metapleural canal (lymph space); M.F = metapleural fold; N = notochord; P = primary bar; PH = pharynx; S = skeleton of dorsal fin; S.A.M = sub-atrial muscle; T = tongue or secondary bar. The thin line with dots in the D.CŒL.C is the cœlomic epithelium. From the cœlomic canal on either side, an outgrowth can be seen connecting it with a primary bar; this is the origin of the cœlomic canal (C.C) that traverses each primary bar (Fig. 54, D, C.C).

ridge of the pharynx (Fig. 55, END), supported by paired chitinous plates which correspond in number and position (Fig. 54, F, E.P) with the primary bars, and since these latter of one side of the body alternate with those of the other side, the **endostylar plates** (E.P) do so as well. The endostylar plates are lined internally with a very tall columnar epithelium (Fig. 54), the cells of which are all ciliated, but those along the middle line possess very much longer cilia than the others. Four groups of cells, two on either side, are characterized by the paleness of their colour in stained preparations; these are groups of mucous cells (Fig. 54, M.S.C), which are continually secreting a slimy material in which the food particles in the stream of water become embedded, and which are thus prevented from passing through the gill-slits, when they would become lost for purposes of nutrition. The long cilia by

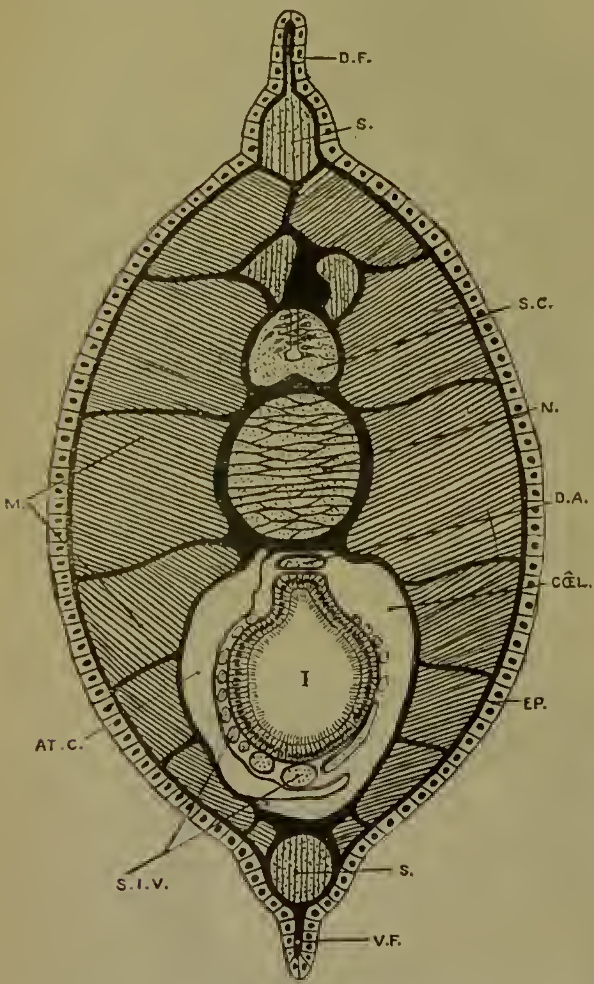


FIG. 56. Transverse section through the mid-intestinal region of *Amphioxus lanceolatus*. AT.C = atrial chamber; CŒL = cœlom; D.A = dorsal aorta; D.F = dorsal fin; EP = epidermis; I = intestine; M = muscle myomere; N = notochord (the black border round it is the notochordal sheath); S = skeleton of fins; S.I.V = sub-intestinal vein (it is of the nature of a fenestrated double membrane, and hence in section appears to consist of a great many separate vessels); S.C = spinal cord; V.F = ventral fin.

their combined movements work the mucus and its contained food-material into ball-like masses which are passed backwards towards the intestine. Beneath the endostylar skeleton there is a spacious tubular cavity (E.C), the **endostylar cœlom**, through which the branchial artery runs.

Posteriorly the pharynx narrows and enters the **intestine** (Fig. 53, INT), which runs a short, straight course to the anal aperture. A little behind the junction of the intestine with the pharynx, the former gives off upon its right side a diverticulum, which runs forward along the same side of the pharynx; this is called the **hepatic diverticulum** (Fig. 53, L), and inasmuch as it is simply an outgrowth of the intestine, it is homologous with the early embryonic liver of all the higher Vertebrates. Both the intestine (Fig. 56, I) and the hepatic diverticulum (Fig. 57, L) are composed of a basement membrane lined with a single layer of columnar epithelium.

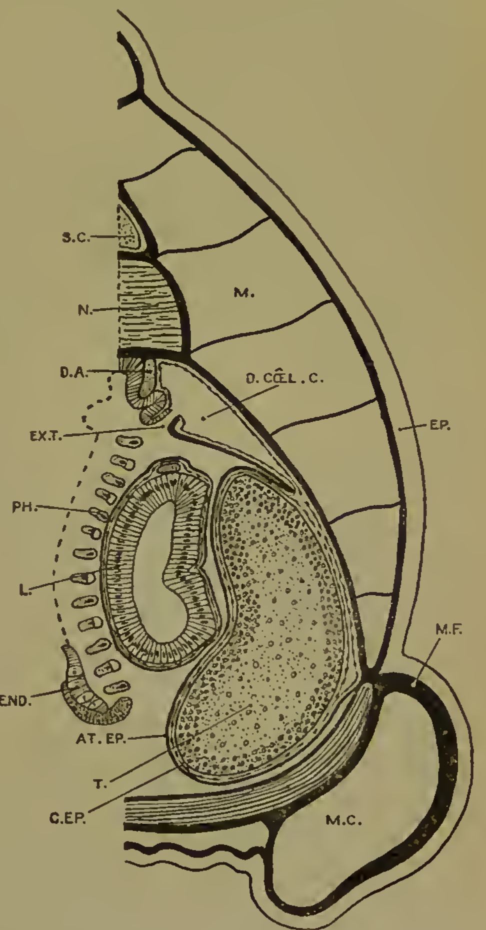


FIG. 57. Transverse section of pharyngeal region of *Amphioxus*, more posterior than in Fig. 55. One side only has been represented. AT.EP = atrial epithelium; C.EP = cœlomic epithelium; EX.T = excretory tubule (nephridial tubule), opening from the dorsal cœlomic canal into the atrial cavity; L = hepatic diverticulum (liver); S.C. = spinal cord. Other letters as in Fig. 55.

Excretory or Renal Organs. The excretory organs are of three kinds: the **nephridia** (Fig. 58), situated at the dorsal ends of the secondary pharyngeal bars; the **brown** or **atrio-cœlomic funnels** placed in the twenty-seventh myotome; and the **renal papillæ** sometimes called **Müller's papillæ**, which occur indiscriminately scattered on the floor of the atrial cavity.

The nephridia are tubular organs bent in the form of an L-shaped loop (Fig. 58), and have several apertures (C.A), ranging from one to seven, opening into the dorsal cœlomic canal (Fig. 57, D.CŒL.C) which runs along the dorsal surface of the pharynx. Upon the lower or ventral surface of the nephridium at the bend of the L there is a single aperture (A.A), situated immediately over a tongue-bar (T.B) and opening into the atrial cavity (Fig. 55, AT.C, and Fig. 57, EX.T). The epithelium lining the nephridia is ciliated, the cilia being very long, and at the cœlomic (C.A) and atrial (A.A) apertures they project beyond and are terminated by little knob-like enlargements.

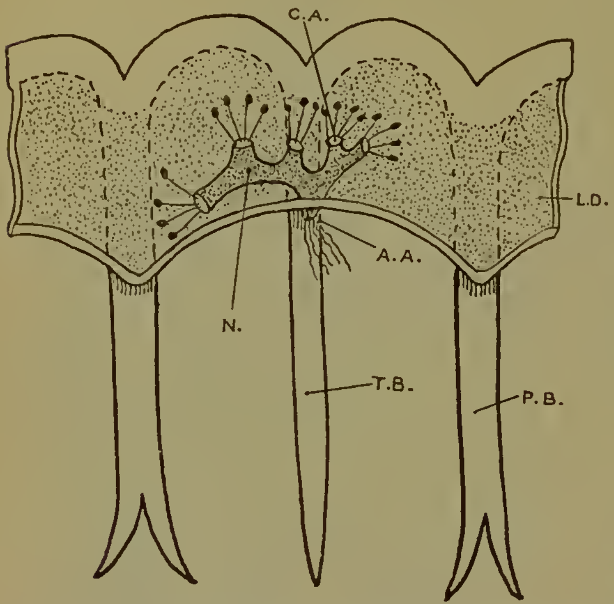


FIG. 58. Side view of two primary bars and one tongue-bar of *Amphioxus*, with a portion of the ligamentum denticulatum and a nephridial tubule. The cut (curved) margin of the ligamentum denticulatum (L.D) is attached, in the intact animal, to the body-wall, and thus forms two chambers, one above (dorsal cœlomic canal) and one below (atrial chamber). The five upper apertures (C.A) of the nephridium thus open into the cœlomic canal, and the lower single one (A.A) into the atrial chamber. The nephridium thus places these two chambers in communication, so that a transverse section passing through the atrial and one of the cœlomic apertures would be represented as in Fig. 57, EX.T, where the thick line with the thin dotted one above it to the left of the tubule represents the cut edge of the denticulated ligament (Fig. 55, L.D). (After Boveri. Altered.) A.A = atrial aperture of nephridial tubule; C.A = cœlomic apertures of same; L.D = ligamentum denticulatum; N = nephridial tubule; P.B = primary bar; T.B = tongue-bar.

The blood supply to these organs (Fig. 59, N) is derived from the cœlomic vessel of a primary bar (Fig. 59, C) and the somatic or external vessel of a tongue-bar (E) which, as they pass through their respective bars, give off, when they reach the level of the nephridium, each a branch, which, splitting into smaller branches over the renal epithelium, anastomose with each other (N). This anastomosis of capillary vessels is called a **glomerulus** (N), and the blood having

passed through it, ultimately reaches the dorsal aorta (D.A) of the same side by means of two, sometimes one, short vessel.

The **renal papillæ** are glandular epithelial tracts in the floor of the atrial cavity, composed of cells more or less ovoid in shape, and the free surfaces of which bear cilia. Two kinds of cells may be distinguished: large, ovoid, clear cells containing highly refractive granules, probably excretory in nature, and between these, small filiform cells of extreme tenuity.

The **atrio-cœlomic** or **brown funnels** are a single pair of funnel-like tubes opening by their expanded mouth into the atrial chamber, and by their smaller aperture into the dorsal cœlom. The cells of which they are composed are laden with a brown pigment.

That all these organs are excretory in nature was proved by Weiss, who fed fully-grown organisms with carmine granules suspended in the sea-water in which they were living. After allowing time for the absorption and passage into the blood-stream of the pigment, the animals were killed and examined by means of transverse and other sections, when it was found that the epithelium lining the nephridia and brown funnels, and the large cells of the renal papillæ, were crowded with granules of the pigment. Moreover, it appears that the cells of the epithelium lining the atrial cavity also possess, to some extent, the power of excreting waste, since they contained carmine granules as well.

The cœlom and atrial cavity. The cavity in which the pharynx lies, and into which the water passes after filtering through the gill-clefts, is not the cœlom or true body cavity, but one which has become shut off from the exterior by the formation of two ectodermic folds, which later unite. It is, therefore, lined with ectoderm, and is called the **atrial cavity** (Fig. 55, AT.C), communicating with the exterior by a single aperture, the **atriopore** (Fig. 53, ATP). The atrial chamber extends round the pharynx from nearly its dorsal limit on one side to the same extent upon the other. Behind the atriopore the atrial cavity extends backwards along the intestine, but it is restricted to the right side (Fig. 56, AT.C). Towards the posterior end of the intestine, however, the atrial chamber ends, and the cœlom is equally well developed on either side of the intestine (Fig. 60, C, CŒL).

Dorsally to the atrial chamber in the pharyngeal region there extends from end to end of either side of the pharynx a tubular canal (Fig. 55, D.CŒL.C), which is separated from it by a double-layered membrane, the **denticulated ligament** (Fig. 55, L.D), so called because

it is thrown into an alternating series of bays and prominences, produced by its attachment to the primary bars, and by its arching over the tongue-bars (Fig. 58, L.D). This canal is the **dorsal cœlomic canal**, sometimes called the **supra-pharyngeal** or **sub-chordal cœlom**. It is in this canal that the nephridia and brown funnels lie, situated upon the dorsal surface of the ligamentum denticulatum. The space running along beneath the endostyle (Fig. 54, F, EC) is also cœlomic, and is called the **endostylar cœlom**; it is connected with the dorsal cœlomic canals by means of the cœlomic canals (C.C), which run through the length of the primary pharyngeal bars.

Posteriorly the dorsal cœlomic canal extends backwards to the posterior end of the intestine (Fig. 56, CŒL), but on the right side it is reduced to a minimum by the encroachment of the atrial cavity (AT.C), and exists merely as a chink-like space between the wall of the intestine and the atrial epithelium; the same is true of it round the hepatic diverticulum (Fig. 57, L). Upon the left side of the intestine it retains its primitive dimensions. The extent of the cœlom in the different regions of the body, and its relation to the atrial cavity, can be most certainly determined by the study of transverse sections.

The Vascular system. The cavities which exist in the dorsal (Fig. 60, A, L.S) and ventral fins in the metapleural folds (Fig. 57, M.C), and between the muscular myotomes, notochord, and nerve cord (Fig. 60, L.S) are lymph spaces. The precise relations between the lymph spaces and the blood-vessels in *Amphioxus* are not certainly known.

The blood system is extremely simple, and in many respects represents the very early embryonic condition of that of craniate Vertebrates.

The **branchial artery** (Fig. 59, B.A) runs in the endostylar cœlom (Figs. 54 and 55, B.A), and gives off a series of alternating short, pulsating **bulbils** (Fig. 59, B), one for every primary bar of the pharynx. Each bulbil branches into three vessels (C, E & I), which run through the bar and ultimately open into the dorsal aortæ. The names given to each of these three vessels, and the exact course which they follow, have already been described in the account of the structure of the gill-bars and of the nephridia.

In the region of the pharynx the **dorsal aorta** (Fig. 59, D.A, and Fig. 55) is a paired artery, one artery lying on either side of the supra-pharyngeal or hyper-pharyngeal groove; along the dorsal surface of the intestine (Fig. 56, D.A) the two aortæ unite to form a single median dorsal aorta. This gives off a number of small branches

(Fig. 59), which break up into capillaries over the intestine, and ultimately open into a vessel lying upon the ventral surface of the intestine, the **sub-intestinal vein** (S.I), which consists of several vessels anastomosing with one another and forming a meshwork, so that in transverse section it appears as a number of distinct vessels

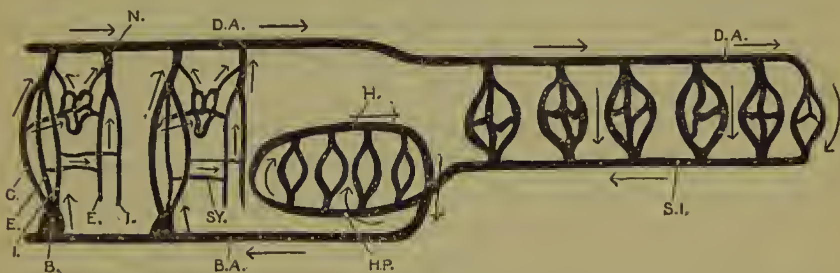


FIG. 59. Diagrammatic representation of the blood-vascular system and circulation of the blood in *Amphioxus*. B = bulbils on branchial artery, B.A.; C = cœlomic blood-vessel of primary bar; D.A = dorsal aorta (the downward bend is at the part where the paired aortæ of the pharynx unite to form the single-median one of the intestine; E = external blood-vessel of gill-bars; H = hepatic vessel; H.P = bepatic-portal vessel; I = internal blood-vessel of gill-bars; N = nepbridial capillaries (glomerulus); S.I = sub-intestinal vein; SY = vessels placing the external and internal vessels of either gill-bars in connexion with each other; they pass through the synapticulæ (Fig. 54, C, s). The arrows indicate tbe direction of the blood-flow.

(Fig. 56, S.I.V); this vein runs forward along the ventral margin (H.P) of the hepatic diverticulum, and breaks up into capillaries that anastomose upon its surface. By the union of these another vein (H) is formed, which is situated upon the dorsal surface of the hepatic diverticulum and opens into the posterior end of the branchial artery; this vein is the **hepatic vein**.

The circulation of the blood. The branchial artery is a contractile vessel, which contracts once in every minute and drives the blood through the vessels in the pharyngeal bars to the aortæ. While passing through the pharyngeal vessels the blood is deprived of its carbon dioxide, and of most of its nitrogenous waste as it passes through the glomeruli upon the nephridia. The blood which enters the dorsal aortæ is thus the purest in the body, and from these it is carried partly forwards, but mostly backwards to the capillaries of the intestine, where, besides nourishing the wall of the intestine, it also absorbs the digested food material which it carries to the capillaries of the hepatic diverticulum. Doubtless the blood undergoes some change here, and the food material which it contains is in some way modified, when it is then taken to the branchial artery to be distributed throughout the body.

Physiologically the branchial artery corresponds to the heart of the higher Vertebrata, and morphologically the fact that it is tubular in form does not much signify, for the heart in all Vertebrates is at first merely a tube situated in the pharyngeal region. Morphologically considered, therefore, the heart of *Amphioxus* remains at the embryonic level of that of all Vertebrates higher in the scale of organization.

The dorsal aorta of *Amphioxus* is also homologous with that of other Vertebrates, but in its anteriorly paired nature it permanently retains an embryonic condition.

The sub-intestinal vein and portal system are repeated in the course of the development of the veins in higher Vertebrata, but in them these undergo profound changes from the condition here represented, and in part are replaced by other vessels.

The vascular system of *Amphioxus*, therefore, retains throughout life the very early embryonic condition of that of higher forms.

The nervous system. The central nervous system consists of a **nerve cord** which, like that of all Vertebrates, is tubular, lying along the dorsal surface of the notochord (Figs. 55, 56, and 60). Its largest diameter is about the middle of its length, whence it tapers to either end. Anteriorly it does not reach as far as the extremity of the notochord (Fig. 53), and posteriorly it almost, but not quite, does so. Two series of nerves are given off from it: a **dorsal series**, the fibres of each of the nerves of which are bound together in a common bundle, and a **ventral series**, the fibres of each of the nerves of which leave the cord independently. The dorsal and ventral nerves which supply a common segment remain independent of each other, and do not unite to form a common spinal nerve as in the dogfish, frog, and rabbit.

Like the spinal nerves of the dogfish, and unlike those of the frog and rabbit, those of *Amphioxus* alternate with each other on either side of the cord, with the exception of the first two pairs, which also differ from the others in other respects, and may possibly represent some of the cranial nerves of higher Vertebrata.

The dorsal spinal nerves, when they leave the spinal cord, run straight outwards through the muscle myotome to which they belong, and just beneath the skin divide into a dorsal and a ventral branch; the former of these passes upwards and supplies the skin of the dorsal surface, and is therefore entirely sensory, while the latter passes ventrally, and in addition to supplying nerves to the skin of the side and ventral surface of the body, gives off also a visceral branch which supplies the pharyngeal bars and the transverse muscles (Fig. 55, S.A.M)

in the floor of the atrium, and is, therefore, both motor and sensory. The ventral spinal nerves are entirely motor, and their fibres upon emerging from the spinal cord spread out in a fan-shaped fashion, and are distributed to the muscle fibres of the myotome which they supply.

The first two pairs of nerves differ in many respects from the others, and are sometimes called the **cranial nerves**. They arise by a single dorsal root, and their distribution is confined entirely to the integument of the snout; their finer terminal branches are characterized by ganglionic swellings placed at their peripheries.

The dorsal spinal nerves arise from the spinal cord immediately behind the posterior dissepiment of the myotome which they supply, while both the cranial nerves arise in front of the first myotome.

The Spinal and Cranial Nerves of Amphioxus contrasted.

Spinal Nerves.	Cranial Nerves.
1. Mixed (motor and sensory).	1. Entirely sensory.
2. Arise by two roots.	2. Arise by a single root.
3. Leave the spinal cord behind the septum of the myotome which they supply, and each nerve is distributed to one myotome.	3. Both arise from the spinal cord in front of the septum dividing the first and second myotome, and their distribution is restricted to the snout.
4. Do not bear ganglionic enlargements.	4. Bear ganglionic enlargements at their distal extremities.

Spinal Nerves of Acrania and Craniota contrasted.

Acrania (*Amphioxus*).	Craniota (*Dogfish*, *Frog*, *Rabbit*).
1. The dorsal and ventral roots of the spinal nerves never coalesce.	1. The dorsal and ventral roots of the spinal nerves coalesce to form a single trunk.
2. The dorsal roots do not bear a ganglionic enlargement.	2. The dorsal roots each bear a ganglionic enlargement.

The nerve tube. The spinal cord of *Amphioxus* is a hollow tube, but along nearly the whole of its length the cavity of the tube is much reduced, and is represented by the small central canal and the dorsal fissure (Figs. 55, 56, and 60). Anteriorly, however, the central canal forms a large dilation, called the **cerebral vesicle**, which is regarded as homologous with the cerebral vesicle of the embryonic nervous system of higher Vertebrates, and which by constriction,

thickening of its wall, and the formation of secondary outgrowths, ultimately gives rise to the complex brain of the Craniota. The anterior wall of the cerebral vesicle contains a patch of pigment, the eye-spot

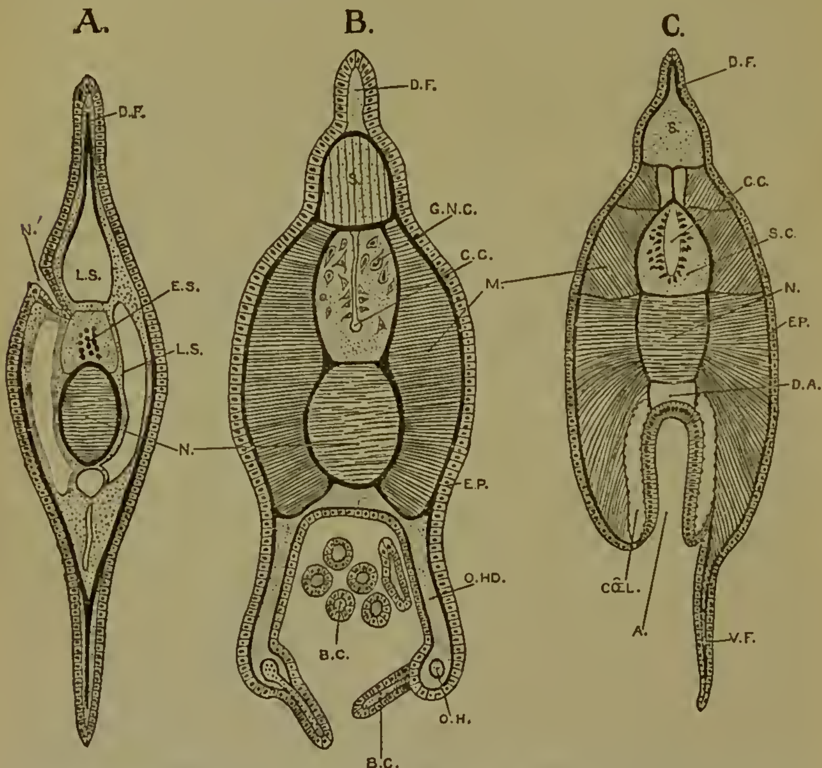


Fig. 60. Three transverse sections through different regions of *Amphioxus lanceolatus*. A. Through the eye-spot and neuropore. B. Through the buccal hood. C. Through the anus. A = anus; B.C = buccal cirri (some are seen cut across transversely and others more or less longitudinally); C.C = central canal of spinal cord; CŒL = cœlom; D.A = dorsal aorta; D.F = dorsal fin; EP = epidermis; E.S = eye-spot (composed of aggregated pigment granules); G.N.C = giant nerve-cells; L.S = lymph space; M = muscle myomeres; N = notochord; N′ = olfactory pit; O.HD = oral (buccal) hood; O.H = oral hoop; S = skeleton of dorsal fin; S.C = spinal cord; V.F = ventral fin.

(Fig. 60, A, E.S), and immediately above this the cavity is prolonged forward as a small median spur-like outgrowth, called the **lobus olfactorius impar.** A similar outgrowth of the cerebral vesicle has been seen in the embryo of *Acipenser sturio* (the sturgeon), and it represents the point at which the central nervous system retains its latest connexion with the ectoderm; in young specimens of *Amphioxus* it is continuous with a funnel-like ciliated pit in the ectoderm, called the **olfactory pit** (Fig. 60, A, N′), from which later it becomes

separated, though the latter persists throughout life. Posteriorly the floor of the cerebral vesicle grows downwards in the form of a pit, called the **infundibular depression**, and it doubtless represents the infundibulum of higher Vertebrates, which in them is a down-growth of the floor of the fore-brain. If this is so, then the cerebral vesicle of *Amphioxus* cannot represent the whole of the same vesicle in higher Vertebrates, since in them the infundibulum arises from the floor of the first of the three vesicles into which the cerebral vesicle becomes divided; and since the infundibular depression in *Amphioxus* is situated at the posterior end of the vesicle, it follows that it is homologous with the fore-brain (the first of the three vesicles) of higher Vertebrates.

A little way behind the cerebral vesicle, but situated at a more dorsal level, there is another dilation of the central canal, or rather of the dorsal fissure, known as the **fossa rhomboidalis**, which is covered dorsally, not by a roof of nervous material, but by a thin membrane. In its relation to the cerebral vesicle, and in the presence of a thin membranous roof, this portion of the neural tube of *Amphioxus* corresponds to the hind-brain or the third vesicle of higher Vertebrates.

There is thus evidence justifying us in regarding this portion of the nerve tube as homologous to the brain of the Craniota, since in its broad features it is similar to the condition presented by the early embryonic brain of the higher Vertebrata.

In transverse section the spinal cord is somewhat triangular, with its angles rounded off, and pierced about two-thirds down from the dorsal surface by the central canal, which is really but the open portion of a much larger canal, the walls of which have become apposed to form the dorsal fissure. Embedded in the wall of the central canal are some elongated cells, the **supporting cells** (Fig. 56), which are continued outwards into processes that pass through the substance of the tube and serve to hold its parts together.

Conspicuous by their large size are the **giant ganglion cells** (Fig. 60, G.N.C) and the **giant fibres** that arise from them. They are arranged in two groups: an anterior one in which the cells lie in the anterior third of the spinal cord, and the fibres from which run backwards, and a posterior one, in which the cells extend through the posterior two-thirds of the cord, and the fibres from which run forwards. Each ganglion cell lies across the middle of the central canal and is multipolar, but one process is much bigger than the others, and constitutes the giant fibre. The course of the giant fibre is

peculiar, since, after arising from the cell, it passes downwards upon one side, then turning, it passes to the other side, and running upwards, turns either backwards or forwards, according as it belongs to the anterior or posterior group, to run longitudinally nearly to the end of the cord.

Running in the nerve cord on either side of the central canal (C.C) there is a bundle of nerve fibres, which at intervals gives off branches that, passing outwards form, in major part, the dorsal roots of the spinal nerves; the remaining fibres of these nerves are derived from small bipolar nerve-cells lying in the neighbourhood of the central canal, one process of each of which goes out to the nerve, and the other passes over and joins the longitudinal bundle of fibres upon the other side.

The exact mode of origin of the ventral roots has yet to be determined, for at their base (the part at which they leave the spinal cord) their fibres appear to end in a granular patch of unknown nature.

The reproductive organs. The gonads (Fig. 57, T), or reproductive glands, are somewhat cubical bodies, metamerically arranged in that region (pharyngeal and anterior intestinal) of the body in which they are developed. They appear to lie in the atrial cavity, but as a matter of fact they only project into it, and in reality are situated in a chamber, **perigonadial cœlom**, derived from the myocœl (cœlomic cavity of a myotome) of the segment next behind that in which they lie, and which at the time of sexual maturity is entirely filled with the sexual elements.

Sexual accessory characters are absent in *Amphioxus*, and the sex can only be determined by examination of transverse sections. The mode of development of the sexual glands presents a feature of considerable morphological importance. In the higher Vertebrates the sexual organs arise as a ridge of the peritoneum (post, p. 355), produced by a local proliferation of its cells, but in *Amphioxus* they arise by a proliferation of the cells, not of the peritoneum, but of the epithelium lining the cavity (myocœl) in which the muscle fibres are developed. The first indication of a sexual gland is a thickening of the septum separating two myotomes, produced by the division and multiplication of the cells forming its posterior wall; the proliferation of cells is confined to a small portion of the septum, i. e. to its most ventral margin, where it is considerably narrowed in the angle formed by the meeting of the integument and the intercœlic

membrane. The multiplication of cells goes on rapidly, and as a consequence the septum becomes pushed forwards and projects into the myocœl of the myotome next in front; very shortly after this projection has commenced, the intercœlic membrane, which is covered on its atrial surface by the atrial epithelium, also begins to bulge downwards into the atrial cavity as a rhomboidal pouch into which later the gonad will come to lie. The projecting portion of the myocœlomic septum, with its developing sexual cells, projects increasingly more into the myocœl of the next anterior segment, and ultimately becomes constricted off from its parent septum, and then lies free in the cavity of the rhomboidal pouch (perigonadial pouch) formed by the projection of the intercœlic membrane, which pushes the atrial membrane (Fig. 57, AT.EP) before it into the atrial cavity.

It follows from this that, although the gonads project into the atrial cavity, they lie not only outside the atrial epithelium, and therefore outside the atrial cavity, but in a pouch which has been derived by constriction from the myocœl. And, since the course of development shows that the myocœl is but a portion of the general cœlom which has become shut off from it, the gonads lie, in the long run, in a pouch constricted off from the general cœlom. Nevertheless, since the perigonadial pouches are formed by the pushing out of the intercœlic membrane which divides the true cœlom from the myocœl, they lie, not in the cavity of the true or general cœlom, but outside of it. They thus occupy a paradoxical position, for they are both within and without the cœlom.

The integument. The integument consists of an epidermis supported by a cutis. Internally the cutis is limited by a layer of flattened cells, the **epithelial layer** or **limiting membrane**, and immediately without this is the **internal layer of the cutis**, composed of a gelatinous material with a few connective tissue-fibres. Outside this is the **middle layer of the cutis**, composed of the same material as the internal, but having in addition radial fibres. The **outer layer of the cutis** is composed of a peculiar material like that forming the skeleton of the pharyngeal bars, and the nature of which (whether ectoderm or mesoderm) is doubtful. The **epidermis** (Figs. 55, 56, 60, EP), which lies outside this, is composed of a *single* layer of columnar cells, which in the larva is ciliated. The single layer of cells, and the presence of cilia, is a character which marks off the epidermis of *Amphioxus* from all other Vertebrates, and links it with the Invertebrates.

Metamerism.

The study of *Amphioxus* affords us a favourable opportunity for considering metamerism. We have seen that the body-wall is composed of a number of muscle segments (Fig. 53), arranged in serial order; each of these segments is called a **metamere**; and because each is a muscular one it is further distinguished as a **myomere** or **myotome**. The myomeres of one side of the body do not lie opposite to, but alternate with those of the other side. This arrangement of organs, in serial segments (metameres), is called **metamerism**.

In *Amphioxus* not only are the muscles of the body metamerically segmented, but also the spinal nerves, the gonads, the primitive cœlom, and in the early stages of development the nephridia, and branchial bars. For every pair of myomeres there is a corresponding pair of spinal nerves, and in the region of the body in which they are developed, a pair of gonads also; and since the myomeres alternate with one another, so do the nerves and gonads.

In the adult animal the cœlom is a continuous channel, and shows no trace of myomeric segmentation; but the study of its development shows that it arises as pouch-like outgrowths of the enteron (primitive gut)—a pair of pouches for every muscular metamere of the body; these pouches grow round the gut and meet in the middle line. From the upper dorsal portion of each pouch the muscle metamere is derived, and retains throughout life the primitive segmentation; but the lower ventral portion becomes confluent with the metameres in front and behind, and ultimately with those of the other side, and there thus arises an unsegmented and continuous cavity, the cœlom.

Primitively the branchial bars are myomerically segmented, i. e. a pair of bars for every muscle metamere, but as development proceeds the number of primary bars increases, and these are added to by the formation of secondary bars, so that the myomeric segmentation is exchanged for a **branchiomeric** one. And, since the nephridial tubules occur over every tongue-bar, and these alternate with the primary bars, it follows that their metamerism is not myomeric but branchiomeric.

Metamerism is very marked among some of the Invertebrate groups: in the Arthropoda, in which group is included insects, crayfishes, prawns, shrimps, centipedes, &c., the exoskeleton and body muscles, the nerve cord, the limbs, the heart and respiratory tubes are metamerically segmented; in the group of Worms, the body muscles,

nerve cord, nephridia, cœlom, parapodia, and setæ are similarly segmented.

Among Vertebrates, *Amphioxus* has retained the character of metamerism more marked than any other, for though lampreys and fishes possess a distinct metameric segmentation of their muscles, and all Vertebrates have a segmental arrangement of their spinal nerves and primitively of their excretory tubules, none of them ever exhibit a myomeric segmentation of their gonads. Among the higher Vertebrata all traces of metamerism, with the exception of that of the spinal nerves and the vertebral column (which is secondary), is lost in the adult; but in them, in the early stages of development, the muscles of the body and the primitive nephridial organs are metameric. Among Amphibia and Reptilia certain of the body muscles retain their primitive segmental character throughout life; the muscle rectus abdominis of the frog (one of the muscles of the ventral abdominal wall) is an easily discovered one, and the student can verify this observation for himself.

There is thus exhibited very pronounced indications of metamerism among the whole of the Vertebrata. And since such a character could not well be independently acquired by each group, seeing how different are their habits, it must be looked upon as of great value in seeking to determine from which Invertebrate stock the primitive Vertebrate first arose; in other words, in looking for the origin of Vertebrates among the Invertebrata, we must seek it in an ancestral stock, that possessed, among others, the character of metameric segmentation.

CHAPTER X

Invertebrata: Cœlomata

THE MORPHOLOGY OF THE ORGANS OF ASTACUS, PERIPLANETA, ANODONTA AND LUMBRICUS

The Exoskeleton and Outer Organization.

The supporting skeleton of the Invertebrata is one derived from the epiblastic layer, and is either a secretion or a cellular layer derived from the epidermis in which calcareous salts may become deposited.

It thus lies outside the body, and serves not only to give support but also protection to the organism. It is thus strongly contrasted with the skeleton of the Vertebrata, which is internal, and, with the exception of the notochord, is always derived from the mesoblast. It may, however, be more or less compared to the enamel of the scales of dogfishes which is developed from the epidermis, while the bony portion of the scale is of mesoblastic origin and is developed later than the enamel.

Astacus. The whole of the body of the crayfish is covered by a hard calcareous skeleton ; the portion that covers the anterior half forms a continuous shield called the **carapace** (Fig. 61), while that covering the posterior half is divided into a number of distinct and freely movable segments.

The carapace is divided upon its dorsal surface, by a **cervical groove** (Fig. 61, C.G), into an anterior **cephalic** or **head portion** and a posterior **thoracic portion.** Anteriorly the cephalic portion is continued forwards as a stout spine-like structure, called the **rostrum** (R), on either side of which, and just beneath it, at its basal end, the stalked **eyes** (Fig. 61) are lodged. The thoracic portion is divided into lateral and middle regions by two grooves running in the long axis of the body, the **cardio-branchiac grooves** (C-B.G) ; these indicate the limits between an internal cavity lodging the heart and viscera and two lateral external chambers containing the gills or branchiæ (Fig. 63, CAR-BR.G). The lateral portion of the carapace that covers in the gills is called the **branchiostegite** (Fig. 61, BS). And, since the whole of the carapace represents both head and thorax, it is, with its contents, spoken of as the **cephalo-thorax** (Fig. 61).

The **abdominal segments** (Fig. 61, 1st–6th, ABD.S) are six in number and all similar. Each segment is a continuous ring-like body (Fig. 62), in which it is convenient to distinguish different parts. The dorsal convex portion is called the **tergum** (Fig. 62, TE) ; the ventral slightly curved part, the **sternum** (ST) ; the lateral, ventrally directed outgrowth at the junction of the tergum and sternum is the **pleuron** (PL) ; and the inwardly directed portion of this as far as the articulation of the appendage is distinguished as the **epimeron** (EPI). On the posterior border of the segment at the junction of the tergum and the pleuron is a small peg-like swelling, which fits into a corresponding depression upon the anterior border of the segment next behind, forming an articulation, upon which the segments may

move as upon a pivot. Since all the segments are similarly articulated, the abdomen as a whole is capable of flexion and extension; it is flexed when the abdomen is doubled upon the thorax, and it is extended when it lies in a horizontal plane continuous with that of the thorax. The movements of flexion and extension are produced by the action of certain muscles. Of these, the **extensor muscles** (Fig. 69, EX.M) lie dorsally to the alimentary canal and arise, one on either side, from the inner surface of the fused thoracic epimera (Fig. 63, EX.M), and passing backward, give off bundles of fibres to the tergum of each segment. The **flexor muscles** (Fig. 69, FL.M) are much more massive and arise, one on either side, from the apodemata (*infoldings*) of the thoracic sternal system (Fig. 63), and, passing backward into the abdominal cavity, the fibres become twisted like the strands of a rope, and are divided into a number of bundles which are inserted into the sternum of each segment.

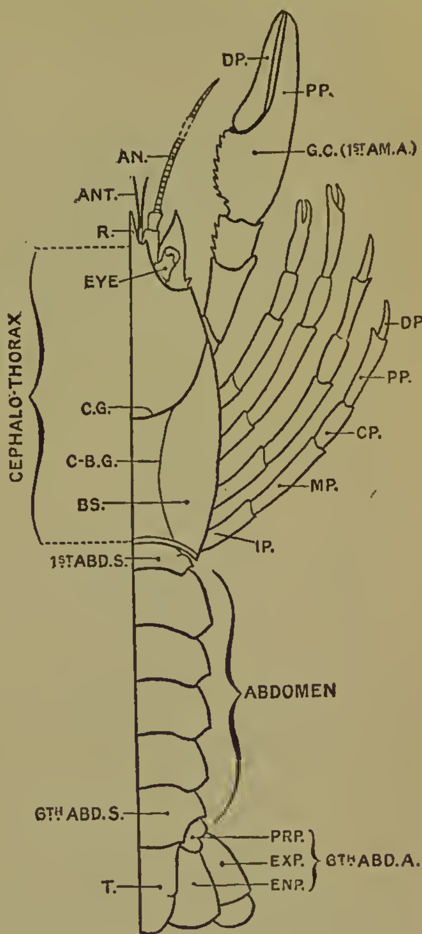


FIG. 61. The exoskeleton of the Crayfish (*Astacus fluviatilis*). As the animal is bilaterally symmetrical, only one half is represented. Dorsal surface. AN = antenna; ANT = antennule; BS = branchiostegite; C-B.G = branchio-cardiac groove; C.G = cervical groove; CP = carpopodite; DP = dactylopodite; ENP = endopodite; EXP = exopodite; G.C = great chela; IP = ischiopodite; MP = meropodite; PP = propodite; PRP = protopodite; T = telson; R = rostrum; 1st & 6th ABD.S = first and sixth abdominal segments; 6th ABD.A = sixth abdominal appendage; 1st AM.A = first ambulatory appendage.

A transverse section (Fig. 63) taken through the thoracic carapace will show that it is built upon the same plan as that of an abdominal segment; but the pleura are much extended and form large lateral down-growths, the **branchiostegites**, which cover and protect the gills (AR.BR & PO.BR), and the epimera

(EP) are more pronounced and form the side-wall of the thoracic cavity.

Examined upon the ventral surface (Fig. 64, A), there are obvious indications that the thorax, like the abdomen, is segmented, for the sternal wall is composed of a number of pieces complicately arranged, but recurring in series or segments. The pieces of each segment have resulted from the calcification of cuticular infoldings called **apodemes**, and since there are four of these, two on either side of the middle line, it follows that each segment is composed of four pieces, i. e. two **endopleurites** (Fig. 64, ENP) and two **endosternites** (ENST). The two endopleurites are attached, one on either side, to the inner surface of the epimeron (EP & Fig. 63, EN.PLR, EP), and at their inner extremity, each is produced into two processes, an anterior (Fig. 64, E, C) and a posterior (E, B), which are attached respectively to the posterior surface of the endosternite next in front and to the anterior surface of that next behind (B, ENST, ENP). The two endosternites (C, ENST) lie immediately on either side of the middle line, and since they are roughly of the form of bent plates with their convex margin outwards, they enclose between them a central cavity, the **sternal canal** (Fig. 63, STR.C). Ventrally, and in the middle line, the endosternites are supported by rod-like plates, the **sterna** (Fig. 63, ST & Fig. 64, A, ST), the anterior ones of which are very narrow and long, but become shorter and broader as we trace them posteriorly.

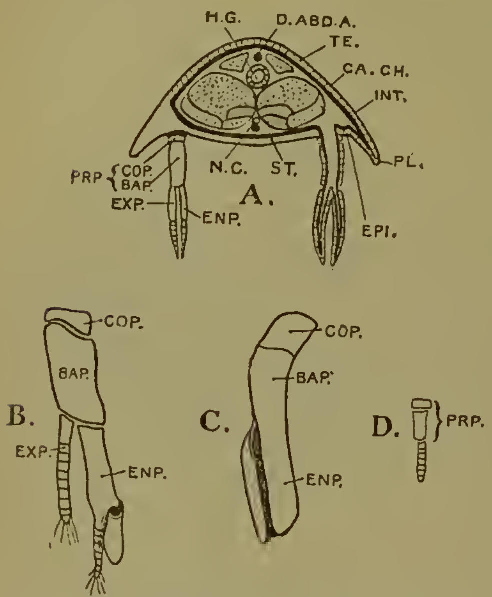


FIG. 62. Exoskeleton of Crayfish (*Astacus*). A. Represents a section of an abdominal segment. B. Second abdominal appendage of the male. C. First abdominal appendage of the male. D. First abdominal appendage of the female. BAP = basipodite; CA.CH = calcified chitin; COP = coxopodite; D.ABD.A = dorsal abdominal artery; ENP = endopodite; EPI = epimeron; EXP = exopodite; H.G = hind-gut; INT = uncalcified integument (hypodermis); N.C = nerve cord; PL = pleuron; PRP = protopodite; ST = sternum; TE = tergum. The extensor muscles are the small dotted patches above, and the flexor muscles the much greater ones below.

The second most anterior of these sternites is very long and narrow and represents the fusion of the three first thoracic sterna. Anterior to

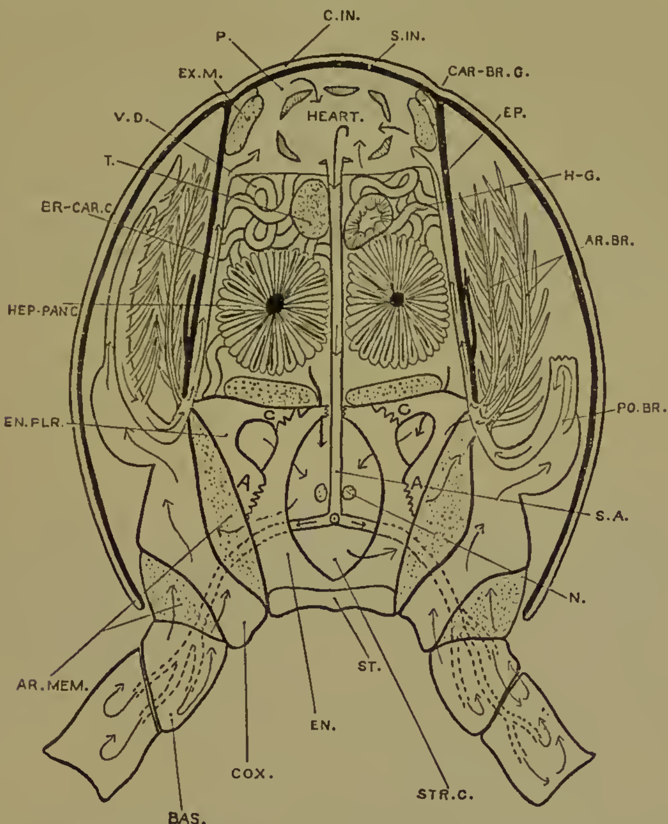


FIG. 63. Transverse-oblique section of Crayfish (*Astacus*) passing through pericardial region of the thorax above and the base of the third ambulatory appendages below. On the right side two arthrobranchæ with the articular membrane from which they arise and the base of a podobranch are shown, but on the left only one arthrobranch but a complete podobranch. The vestigial pleurobranch of either side is shown as a black line arising from the epimeron. A and C on the endopleurite EN.PLR are placed on the same processes as the same letters in Fig. 64. AR.BR = arthrobranchæ; AR.MEM = articular membrane; BAS = basipodite; BR-CAR.C = branchio-cardiac canal; CAR-BR.G = cardio-branchiac groove; COX = coxopodite; C.IN = calcified integument; EN = endosternite; EX M = extensor muscle; EP = epimeron; H-G = hind-gut; HEP-PAN.G = hepato-pancreatic gland; N = nerve cord; P = pericardium; PO.BR = podobranch; S.IN = soft integument (hypodermis); ST = sternite; STR.C = sternal canal; S.A = sternal artery; T = testis; V.D = vas deferens.

this is an arrow-headed broad plate, which represents the fused two posterior sterna of the head. The ventral margins of the endopleurites and the endosternites form an articular surface (Fig. 63) upon which the thoracic appendages (COX) move, while their processes and internal surfaces serve for the origin of the muscles which move them.

THE LIMBS OR APPENDAGES.

The limbs of the crayfish consist of a number of jointed appendages (Fig. 61) serially arranged in pairs. The presence of the jointed limbs is a characteristic feature of the phylum **Arthropoda**, to which the crayfish belongs, and is one which it shares in common with insects, water-fleas, carp lice, scorpions, spiders, &c. In some Arthropoda (centipedes and *Peripatus*) nearly all the appendages are alike, and it is easily seen that the jaw apparatus and the antennæ are but modified legs. The student will, therefore, not be surprised to learn that the mandibles and foot-jaws of the crayfish are but limbs which have become modified for purposes of manducation.

The appendages of the Arthropoda are dermal outgrowths of the body-wall, into which muscles become intruded. The tubular outgrowth becomes hardened in parts and forms the different segments of the limbs, while the uncalcified or unchitinized parts form the flexible joints.

If we leave the eye-stalks out of consideration as being doubtfully modified limbs, the crayfish possesses altogether nineteen pairs of appendages, which are all referable to a **biramose type**, i.e. they consist (Fig. 62) of a basal joint, the **protopodite** (PRP), with two branches arising from it, an inner **endopodite** (ENP), and an outer **exopodite** (EXP). These appendages are named and arranged as follows:—

Cephalic Appendages.	First. One pair of antennules. Second. One pair of antennæ. Third. One pair of mandibles (one mandible on either side of the oral aperture). Fourth and fifth. Two pairs of maxillæ.
Thoracic Appendages.	First to third. Three pairs of maxillipedes. Fourth to eighth. Five pairs of ambulatory or walking legs.
Abdominal Appendages.	First to fifth. Five pairs of swimmerets. Sixth. One pair of 'flappers.'

Of these appendages, the first five pairs are regarded as belonging to the head, the next eight as belonging to the thorax, and the last six as belonging to the abdomen.

In the abdominal region, the primitive segmentation of the body is retained in virtue of the freely movable segments (Fig. 61), to each of which there is attached one pair of appendages; in the thorax, the segments have completely fused on the dorsal surface, though

on the ventral surface, distinct evidence of segmentation is still retained in the form of the laterally compressed sterna and the presence of the serially arranged limbs; the first thoracic sternum, however, instead of being related to a single pair of appendages like all those behind, lies between the bases of the three pairs of maxillipedes and, therefore, probably represents the fusion of three sterna. When we pass to the head, the only traces of segmentation which remain are the presence of the serially arranged appendages. Hence as we pass forwards from the hinder region of the crayfish, we pass through portions of the body which become more specialized as we proceed, the specialization consisting of the fusion of segments which were primitively free. The abdomen retains its primitive segmentation; the thorax has partially lost it; the head completely so, if we leave out of consideration the presence of the appendages. Moreover, the abdomen is distinctly segmented from the thorax, but the latter and the head have become confluent.

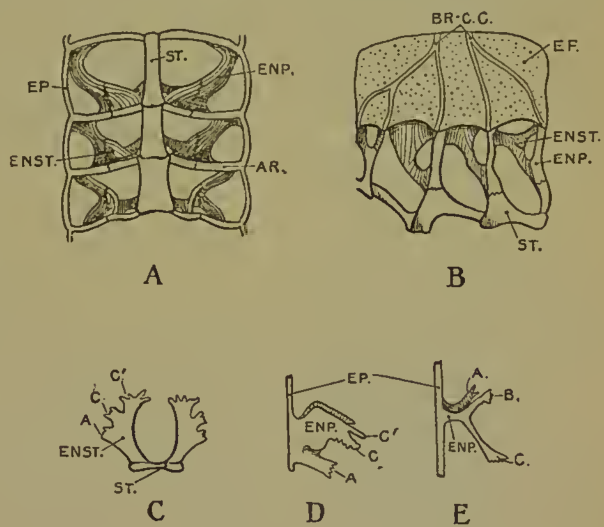


FIG. 64. The endophragmal (cephalo-thoracic sternal) system of the Crayfish (*Astacus*). A. Ventral view. B. Side view. C. Anterior view of a pair of endosternites. D. Anterior view of an endopleurite. E. Dorsal view of an endopleurite. The processes C, C′, and A of the endopleurites are dovetailed in the intact skeleton with the processes C, C′, and A of the endosternites. The parts of the system may be easily disarticulated by boiling it for a few minutes in caustic potash. AR = arthrophragm (articular plate for the appendages); B = posterior process of endopleurite; BR-C.C = branchio-cardiac canals; C = anterior process of endopleurite, but a lateral process in endosternite; C′ = processes of the endosternites and endopleurites; ENP = endopleurite; ENST = endosternite; EP = epimeron; ST = sternite.

Thus the study of the skeleton confirms the conclusion we shall adduce when dealing with the nervous system (p. 257). The crayfish is a highly specialized arthropod, which has attained greater rigidity of parts, greater precision in obtaining its food, and greater protection for itself, by the fusion of segments that were free in the ancestors whence it arose.

Not only have the body segments become specialized but also the appendages. As a central type of limb, with which to commence our study, we may consider the third, fourth, or fifth abdominal swimmerets (Fig. 62, A). Each is articulated to the margins of an articular cavity situated on either side of the sternum between its outer extremity and the epimeron, by an arthrodial (articular) membrane. This latter is simply an uncalcified portion of the integument. Each swimmeret consists of a basal portion, the **protopodite**, composed of a proximal, very small joint (COP), and a distal, larger one (BAP), which supports two many-jointed filaments, an inner **endopodite** (ENP), and an outer **exopodite** (EXP). The appendages of the sixth abdominal segment are modified into '**flappers**' (Fig. 61, 6th ABD.A) which, with the modified seventh segment, called the **telson** (Fig. 61, T), serve as propelling organs in the retrograde movements of the animal. In the 'flappers' the protopodite (PRP) is very short and single-jointed, and the endopodite and exopodite are flattened and broadened laterally, while the latter is also divided into a larger proximal, and a smaller distal joint.

In the female (Fig. 62, D), the first abdominal appendage is reduced to a mere filament. In the male, the first and second abdominal appendages are modified to act as sperm-conducting channels by which the sperm is deposited upon the triangular area between the two pairs of the fourth and fifth ambulatory appendages of the female thorax. The second abdominal appendage (Fig. 62, B) consists of a two-jointed protopodite (COP, BAP) bearing an exopodite (EXP) and a modified endopodite (ENP) ; the distal end of the latter is rolled upon itself in the form of an imperfect tube and bears a small, distal many-jointed filament near its free extremity. The first abdominal appendage (Fig. 62, C) is devoid of an exopodite, and the endopodite and protopodite have fused to form an imperfect tubular structure, which is twisted upon its long axis.

The thoracic appendages may be divided into an anterior three pairs of foot-jaws or **maxillipedes** (Fig. 69) and a posterior five pairs of walking legs or **ambulatory appendages** (Fig. 61). The fifth ambulatory appendage consists of a two-jointed protopodite; the proximal joint is called the **coxopodite** (Fig. 63, COX), and bears a gill (PO.BR) and a bunch of filaments, the **coxopoditic setæ** ; the distal joint is the **basipodite** (BAS) and supports the endopodite. The latter is divided into five joints, which are named, proceeding from the proximal to the distal joint, **ischiopodite** (Fig. 61, IP),

meropodite (MP), carpopodite (CP), propodite (PR), and dactylopodite (DP).

In the male, the coxopodite of the fifth ambulatory limb is pierced by the **genital aperture**, while in the female this aperture pierces the corresponding joint of the third ambulatory appendage.

The fourth ambulatory appendage is like the fifth, but the second and third differ from them in that the propodite has grown forward at its distal extremity so as to form a biting claw-like structure with the dactylopodite (Fig. 61).

The first ambulatory appendage is called the **great chela** (Fig. 61, G.C), and is distinguished from the others by its great size, especially of the propodite (PP) and dactylopodite (DP), and by the fusion of the ischiopodite with the basipodite. The great chela is alike a defensive, offensive, and prehensile organ, and it owes its characters to the presence of the large claw and the strong muscles which work it; these are lodged within the enlarged basal portion of the propodite (Fig. 65, PR), and are two in number: a larger **adductor muscle** (AD.M), which by its contraction closes the claw, and a smaller **abductor** (AB.M), which opens the claw.

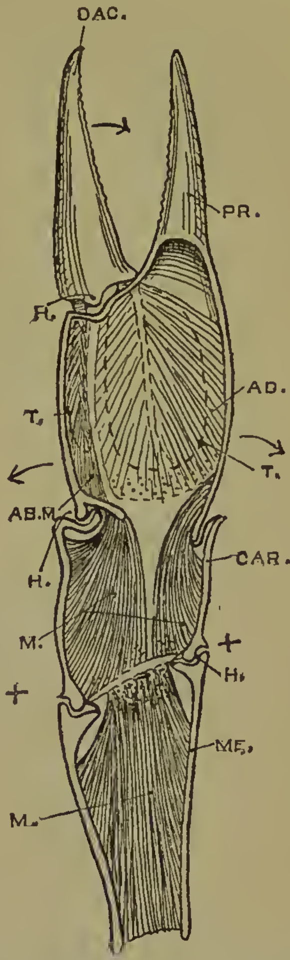


FIG. 65. The great chela of the Crayfish (*Astacus*), with one wall of the propodite, carpopodite, and meropodite removed to show articular joints and muscles. The arrows indicate the direction in which the joint moves, and the + indicates that it moves towards or away from the observer. AB.M = abductor muscle; AD.M = adductor muscle (the dotted line represents the chitinous plate (tendon) to which the muscle is inserted); CAR = carpopodite; DAC = dactylopodite; H = hinge-joint; M = muscle; ME = meropodite; PR = propodite; T = tendon.

In all the ambulatory appendages an exopodite is absent.

The **third maxillipede** (Figs. 69 & 66, 3rd MAX) lies immediately in front of the great chela and consists of a protopodite (Fig. 66, **1**, CO, B), endopodite, and exopodite. The protopodite is composed of a coxopodite with a gill-bearing **epipodite** (EP) and coxopoditic setæ, and a basipodite (B) supporting the endopodite and exopodite (EX). The latter is small, with

a proximal, undivided joint, and a distal many-jointed one. The endopodite consists of a large ischiopodite (IS) fused with the basipodite (B), of a meropodite (M), carpopodite (C), propodite (P′), and dactylopodite (D). The **second maxillipede** (Fig. 66, **2**) is similar to the third, but the endopodite is smaller, and the exopodite is relatively larger; the smallness of the endopodite is due to a reduction in size of the ischiopodite, which is not fused with the basipodite, and also of the carpopodite. The **first maxillipede** (Fig. 66, **3**) is very much modified: its various parts are flattened and lamellar in form, no gill is present, and the endopodite (E) is reduced to a very small, conical plate. The basipodite (B) and coxopodite (CO) are flattened and expanded, and the latter bears a membranous expansion, the epipodite (EP), similar in all its relations to the gill-bearing plate of the other appendages which bear gills.

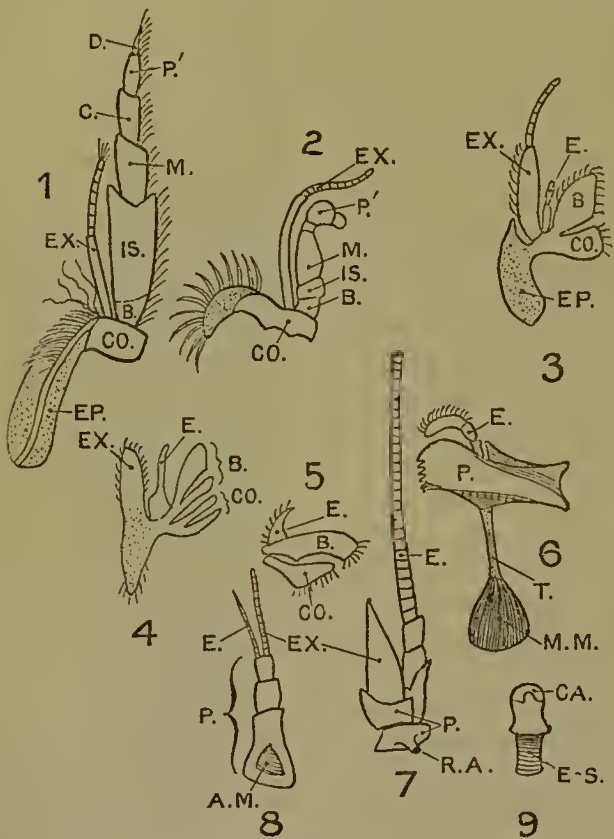


FIG. 66. The appendages of the Crayfish (*Astacus*). 1. Third maxillipede. 2. Second maxillipede. 3 First maxillipede. 4. Second maxilla. 5 First maxilla. 6. Mandible. 7. Antenna. 8. Antennule. 9. Eye-stalk and eye. A.M = auditory membrane; B = basipodite; CA = cornea; C = carpopodite; CO = coxopodite; D = dactylopodite; E = endopodite; EP = epipodite; EX = exopodite; E-S = eye-stalk; IS = ischiopodite; M = meropodite; M.M = mandibular muscle; P = protopodite; P′ = propodite; R.A = renal aperture; T = tendon.

The **second maxilla** (Fig. 66, **4**) is also much modified, its various parts being flattened and lamellar. The coxopodite (CO) and basi-

podite (B) are partially divided into two, the endopodite (E) is relatively large, and the exopodite (EX) has fused with the epipodite to form an elongated, blade-like organ, called the **scaphognathite**, which by a peculiar sculling movement, is instrumental in maintaining a current of water through the gill-chamber. The scaphognathite lies in a short canal, formed by the anterior portion of the branchiostegite, the anterior limits of which are marked by the cervical groove, and since the branchial chamber is open below and behind along the ventral and posterior margins of the branchiostegite, the sculling movement of the scaphognathite results in the extraction of water from the gill-chamber, with the consequent inflowing of external water in order to replace it. The **first maxilla** (Fig. 66, 5) is very much reduced: the coxopodite (CO) and basipodite (B) are soft, flat, membranous plates; the endopodite (E) is of the same nature, and appears only as a very small appendage of the basipodite; an exopodite and epipodite are absent.

The **mandibles** lie on either side of the oral aperture (Fig. 69). The protopodite (Fig. 66, 6, P) forms a very stout, unjointed structure, with a serrated, inner margin; it possesses two articular peg-like processes, and is moved upon these by a very strong muscle (M.M), which arises from the dorsal portion of the cephalic thorax, and is inserted into the protopodite by a long and strong tendon (T). The endopodite (E) is a small, three-jointed, curved structure, called the **palp**.

In front of the mandibles, the sternal surface of the head is directed forwards, not downwards like that of the rest of the body, in consequence of which the appendages attached to it are also directed forwards. These consist of the antenna and the antennules, and among which, by some authors, the eye-stalks are also included.

The **antenna** (Figs. 69 & 66, 7) consists of a two-jointed protopodite (P), the coxopodite of which is pierced by the **renal aperture** (R.A); the exopodite (EX) is in the form of a pointed spear-head-like body termed the **scaphocerite**. The endopodite (E) is composed of two proximal, large joints, supporting a many-jointed filament.

The **antennule** (Fig. 66, 8) is composed of a three-jointed protopodite (P) the basal one of which lodges the auditory sac (A.M), and the distal one supports a multi-jointed endopodite (E) and exopodite (EX).

Microscopic Structure of the Exoskeleton.

The exoskeleton of the crayfish is a calcified cuticle. The cuticle arises either as a secretion of the cells of the epidermis, or as the

result of the chemical transformation of the outer layer of their protoplasm. It consists chemically of a substance allied to horn, called **chitin**, but differs from horn in that it is not cellular in structure: horn is composed of cells the protoplasm of which has become chemically and physically altered, while chitin is only a derivative of cells—is not itself composed of cells.

Within the substance of this chitinous investment calcareous salts may be deposited in certain parts, leaving other parts uncalcified; the former constitutes the exoskeleton, the latter the articular membranes, by means of which different portions of the skeleton are held together and are rendered capable of movement upon each other.

Microscopical examination of a transverse section through a calcified portion of the integument shows that it consists of three layers: an **epiostracum**, **ectostracum**, and **endostracum**. The first of these layers is outermost, very thin and wrinkled; the second is somewhat transparent, is immediately subjacent to the first, and at times presents a finely-laminated appearance, and is traversed by a number of wavy, vertically arranged striæ; the third and innermost layer constitutes the greater thickness of the whole, and like the ectostracum is laminated though more distinctly, and is traversed by radially disposed and wavy striæ. Examination of a section made parallel to the surface of the integument shows that the wavy striæ are the optical expression of minute tubular canals piercing the thickness of the exoskeleton, and that it is composed of so many columns, corresponding in number and form to the cells of the ectoderm.

At various parts of the exoskeleton there project bunches of hair-like processes, called **setæ**. These always arise from the base of a depression in the cuticle, and consist of jointed, usually two-jointed structures; some have smooth surfaces, others are variously tuberculated, and some produce lateral branches. Passing through the thickness of the cuticle, immediately beneath the depression from which the seta arises, is a wide tubular canal, into which the ectoderm projects, and which may also extend into the cavity of the seta itself. The setæ and tubercular processes are thus tubular foldings of the ectoderm and cuticle, just as the endosternites and endopleurites are calcifications of the infoldings of the ventral wall of the thoracic ectoderm.

The Cockroach. The exoskeleton is composed of uncalcified chitin, having the chemical composition of $C_{15}H_{26}N_2O_{10}$. It is made

up of a number of plates called **sclerites**, which may be united together by sutures, to form rigid plates. Externally the body of the cockroach is divisible into **head**, **neck**, **thorax**, and **abdomen**. Apart from its appendages the head has lost all trace of segmentation, though the thorax and abdomen are distinctly segmented. The thorax in all insects consists of three segments named from before to behind, the **prothorax**, **mesothorax**, and **metathorax**. Each of these bears a pair of ventral appendages or thoracic legs, and the last two segments a pair of dorsal outgrowths or wings on each. The exoskeleton of the thoracic segments consists in each of a dorsal plate, the **tergum**, and of a ventral plate, the **sternum**. The tergum of the prothorax is called the **pronotum**, that of the mesothorax the **mesonotum**, and that of the metathorax the **metanotum**.

The wings are of the nature of outfoldings of the ectoderm and its chitinous investment, from the antero-lateral corners of the meso- and metanotum. In *Periplaneta orientalis* (our common black-beetle) the wings are fully developed only in the male; in the female the anterior pair of wings are represented by a pair of small movable plates, and the posterior pair not at all. In the American Cockroach (*Periplaneta americana*) and the German Cockroach (*Phyllodromia germanica*) both pairs of wings are present in both sexes, and are as fully developed in the female as the male. The anterior pair of wings—those arising from the mesonotum—are brown and firm in texture, oblong in form, and with rounded corners. The posterior pair are shorter, broader, thinner and flexible, and when not in use, lie folded away beneath the anterior ones: hence the latter are called **wing-covers** or **elytra**.

The thoracic legs are all alike, except that they increase in size from before backwards. Each consists of a large, basal, conical joint, the **coxa**, followed by a short curved one, the **trochanter**, which is succeeded by a narrow, elongated **femur**, this by a shorter **tibia**, and the whole terminated by a five-jointed **tarsus**.

Photographs taken while insects are in locomotion show that they move forward by the simultaneous movement of three of the legs, the remaining three legs meanwhile supporting the insect. The legs are thus divided into two sets, and each set consists of the first and third legs of one side and the second leg of the other; each set, when at rest, thus forms a tripod.

The **abdomen** consists of ten segments, each composed of a dorsal sclerite (**tergum**), and a ventral one (**sternum**), united by a lateral,

flexible membrane (pleuron) on each side. The first sternite is reduced, and the second is cut out in front and on either side to accommodate the basal joints of the backwardly directed, last pair of thoracic legs. In the female only seven sternites are visible, and nine in the male. In the female the seventh sternite is produced backwards into a boat-like structure, in which the hinder portion of the keel is split, so as to allow expansion at the time of the expulsion of the egg-case; the backward prolongation of this sternite hides those of the eighth and ninth, and forms with them a pouch-like excavation in which they constitute the roof and front wall, while the seventh forms the floor. This pouch is the **brood-pouch**, and in it the eggs are deposited one by one in an egg-case formed by the secretion of the colleterial glands. From the ninth sternum there projects into the pouch a series of six chitinous processes, called the **gonapophyses**, which manipulate the egg-case in the course of its formation, and guide the eggs as they leave the aperture of the oviduct.

In the male the eighth and ninth tergites are telescoped within each other, and partly within the seventh, and the tenth sternite is telescoped within the ninth, forming a shallow pouch into which the anus and genital aperture open. On either side of the genital aperture there is a series of chitinous hooks, the **gonapophyses**, symmetrically arranged and arising from the ninth sternite; they are copulatory organs, accessory to the act of reproduction.

In both male and female there is, on either side of the anus, a small cuticular plate called the **podical plate**; they perhaps represent the tergum of an eleventh segment. Arising from the lateral edges of the tenth tergum, in male and female, is a pair of many-jointed appendages, the **cerci** or **cercopods**, which probably represent the modified limbs of the eleventh segment. In the male there is a pair of processes arising from the ninth sternum called **stylets**; they may represent modified appendages.

With the exception of the questionable cerci and stylets, the abdomen bears no appendages, and the absence of such from this region of the body is characteristic of nearly all insects. In some bristletails, however, all the segments of the body bear small pairs of limbs; and in the embryonic stages of the cockroach abdominal processes appear which are in every way comparable to the early rudiments of the thoracic legs, and undoubtedly represent vestigial abdominal legs. Such vestiges also appear in many other insect embryos, such as the water-beetle (*Hydrophilus*) and others. Moreover, in other tracheate

arthropods, i.e. the myriapoda and prototracheata, the abdominal segments all bear appendages. Hence we must regard insects as the most highly specialized arthropods which have been derived, by evolution, from forms in which there was no division into thorax and abdomen, and in which all segments of the body were limb-bearing.

The head and its appendages. The head of the cockroach is flattened from before to behind, which gives it the appearance of being turned down. It is composed of several sclerites united together, of which that forming the front of the head is called the **clypeus**, those the sides the **genæ**, and that the back and crown of the head the **epicranium.** At the back of the head is a large shield-shaped opening, the **occipital foramen**, through which the nerve cord, œsophagus, and air-tubes pass to reach the thorax; the neck is strengthened by seven sclerites, of which two are ventral, one dorsal and median, and four lateral. The pair of large compound eyes are borne upon the genæ at the side of the head and just behind the large feelers or **antennæ**, which arise from the lateral portions of the clypeus at the junction of that with the crown. The clypeus is prolonged downwards in the middle line and immediately in front of the mouth in the form of an upper lip or **labrum**, behind which is the membranous roof (**epipharynx**) of the mouth, the seat of the sense of taste.

The **mandibles** are the second pair of head appendages, and are situated on either side of the oral aperture; they are serrated on their inner margins, and are articulated in part with the lower, lateral portion of the epicranial sclerite, and in part with the border of the clypeus; they are moved by powerful muscles situated within the head, their movements being from side to side.

The anterior or first pair of maxillæ are situated behind the mandibles and, like them, are paired. Each half consists of a basal segment, the **cardo**, projecting from the head somewhat horizontally, followed by a stout, vertical segment, the **stipes**; at the lower extremity of the latter are borne three structures : the **palps**, a five-jointed filament on the outside, and within the other two arranged one behind the other, an anterior lobe, the **galea**, and a posterior blade, the **lacinia.** The palps are used as organs of touch, and the lacinia as accessory, masticatory organs.

The posterior or second pair of maxillæ are similar to the first, but differ from them in that the cardites (cardo) are fused to form

a single plate, the **submentum**, while the stipes are similarly fused to form the **mentum**, which is distally slightly separated, each limb bearing its galea and lacinia; the palps are three-jointed, and are borne upon a slight process (**palpiger**) on either side of the mentum. The posterior pair of maxillæ are sometimes called the lower lip or **lamium**. We thus learn that the head of the cockroach bears four pairs of appendages, i.e. antennæ, mandibles, and first and second pair of maxillæ; and since the segments behind, and the body segments of all other arthropods, only bear one pair of appendages for each segment, we are justified in the conclusion that the head of the cockroach represents a fusion of four segments. Indeed the study of embryology leads us to the conclusion that a larger number of segments than this are involved.

In front of the posterior maxillæ is a fold of the skin of the mouth, known as the **lingua** or **hypopharynx** (*tongue*), and on the under surface of this the salivary glands open.

Situated within the head capsule, and formed by the infolding of the skin of the back of the head, is a complex skeleton, the **tentorium**, which serves to give attachment to various muscles that move the head and jaws.

Fresh-water Mussel. The exoskeleton of the mussel consists of two valves, disposed right and left of the body, and formed by the glandular secretion of the thickened, ventral margin of two membranous outgrowths of the body-wall, called the **pallium** or **mantle** (Fig. 74, P). The two valves are articulated with each other along the dorsal line; in this region the margin of the shell (Fig. 67, L) is almost straight, and there are no 'teeth' as in other bivalve molluscs. This margin of the shell is called the '**hinge-line**,' and there extends along its length, between the two shells, a tough, elastic **ligament** (L). In addition to holding the valves together, the ligament serves to divaricate (open) them, when the muscles which close them are relaxed. These muscles are two in number, one at either end of the shell, and are called the **posterior** (Fig. 67, POS.A.I) and **anterior adductor** (ANT.A.I) **muscles**; they stretch from valve to valve through the body of the animal, and the parts where they are inserted into the shell are marked by '**impressions**' (Fig. 67, POS.A.I, ANT.A.I). In addition to the impressions of the adductor muscles, there are also those of muscles concerned in the movements of the animal's foot; these are, the posterior (POS.R.I) and anterior (ANT.R.I) retractor and the protractor muscle (P.I) impressions.

The line of attachment of the pallium is also indicated by an impression, the pallial line (P.L).

Stretching away from the muscular impressions and converging to a common point are a number of lines; these represent the path of shifting of the muscle as the shell grew, for the mussel, like every other organism, starts from a small beginning. In the larval stage, the shell is a mere speck, and as the animal grows, the thickened edge of its mantle adds fresh material to the existing shell, and so it becomes bigger; and with enlargement of the shell, there is a correlated necessity for the adductor and other muscles to be outwardly moved, and the paths along which they have travelled in this outward shifting are indicated by these converging lines (Fig. 67, L. OF S).

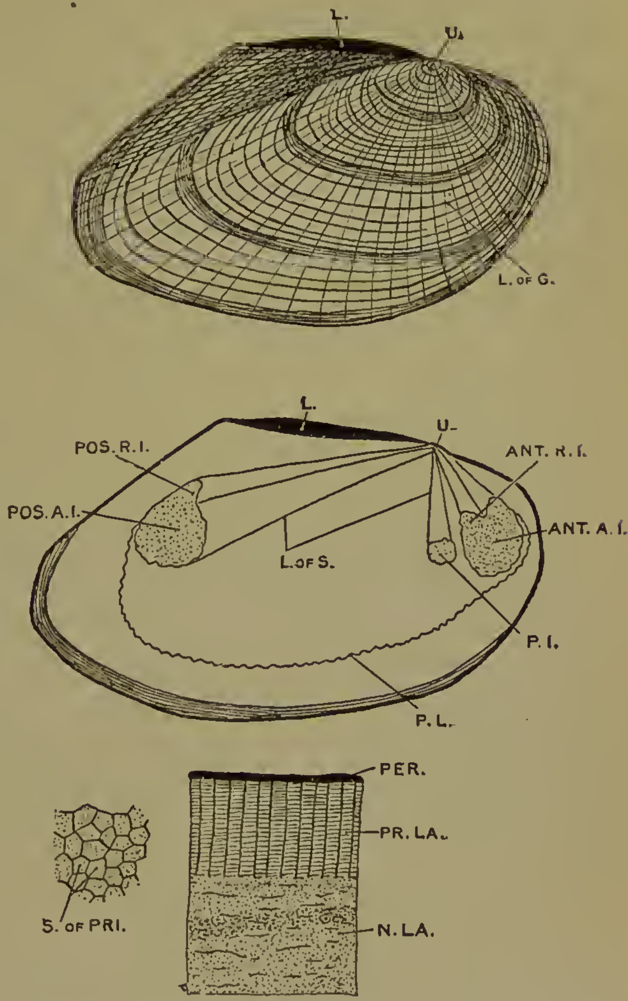


FIG. 67. Exoskeleton of the Fresh-water Mussel (*Anodonta*) The upper figure represents the external surface of the right, and the middle one the internal surface of the left shell. The larger lower figure represents a transverse, and the smaller a tangential section of the shell seen under the one-sixth objective. ANT.R.I = anterior retractor impression; ANT.A.I = anterior adductor impression; L = ligament; L. OF G = lines of growth; L. OF S = lines of shifting; N.LA = nacreous or pearly layer; PER = periostracum; POS.A.I = posterior adductor impression; POS.R.I = posterior retractor impression; PR.LA = prismatic layer; P.L = pallial line; P.I = protractor impression; S. OF PRI = tangential section of prisms; U = umbo.

The original larval shell, around which all the other has been formed, forms an excentric point upon the shell, towards which the various markings of the shell converge: this point is called the **umbo** (Fig. 67, U). The various increments added to the shell in the course of its growth are indicated by well-marked concentric, and by less strongly developed radial **lines of growth** (Fig. 67, L. OF G).

The bluntly-rounded end of the shell is the anterior end, the more tapering the posterior end; the hinge-line is, therefore, the dorsal margin, and the pallial line the ventral margin of the shell.

Examined microscopically by means of transverse sections, the shell is seen to be composed of three layers: an outer, chitinous, uneven **periostracum**; a middle, calcareous, **prismatic layer**, and an inner, calcareous, granular, **nacreous** or **pearly layer**. The prismatic layer (Fig. 67, PR.LA) is composed of calcium carbonate and calcium phosphate; this is laid down in the form of vertical prisms, each of which shows a faint transverse striation, and which in transverse sections of the shell appear as columns, and in tangential ones (parallel to the surface of the shell) as hexagonal or polygonal plates. The nacreous layer (N.LA) is chemically similar to the prismatic, but it consists of a finely granular substance, with innumerable microscopic cracks, which, by interference with the light rays, produce the iridescent, pearly appearance of the inside of the shell.

The Earthworm. The exoskeleton of the earthworm consists of a very thin cuticle, with two pairs of setæ in every segment of the body except the first. The cuticle is a homogeneous chitinous layer formed by the secretion of the epidermal cells (Fig. 76, B, EP.C). Seen in surface view it exhibits a number of intersecting faint lines, with slight nodal enlargements where they cross one another (C).

The **setæ** (Fig. 76, A, S) are chitinous spindle-shaped rods, formed by the secretion of the epidermal cells in the bottom of a follicular invagination of the epidermis. They are arranged in two series along the length of the body: two ventral and two ventro-lateral pairs in each of the body segments. Each seta in each pair is moved by three muscles; a pair of **protractor muscles** (Fig. 76, A, P.M), which when they contract project the setæ outwards, and two **retractor muscles** (R.M), one of which pulls it inwards and in one direction, and the other inwards and in the opposite direction.

The body of the earthworm is divided externally into segments by deep annular constrictions; this external segmentation corresponds to a segmentation of some of the internal organs. Each segment is

marked externally by a shallower groove, lying midway between every two of the deeper constrictions; it is only skin deep and divides each segment into two **annuli**; it does not indicate any internal segmentation.

The mouth opens on the first segment, the anterior annulus of which hangs over it, forming the **prostomium**. The anus opens on the last segment. With the exception of the first two and the last three, each segment is pierced between the ventro-lateral and lateral pairs of setæ, on either side of the body, by a minute aperture, that of the **nephridia** (Fig. 76, A, NA). Along the mid-dorsal line, each segment is pierced in its middle by a **dorsal pore** (Fig. 76, D.P), which places the cœlom in direct communication with the exterior. Between the ninth and tenth, and the tenth and eleventh segments, are the apertures of the seminal receptacles (Fig. 78). On the ventral surface of the fourteenth segment are those of the oviducts, and on the fifteenth those of the vas deferens, surrounded with tumid lips.

The **epidermis** consists of a single layer of columnar cells (Fig. 76, B, EP.C), some of which at frequent intervals become chemically altered and enlarged to form **goblet cells** (G.C); these are unicellular glands, and secrete the slimy mucus with which the body is covered and by which the wall of the burrow becomes invested. Beneath the epidermis is the muscular body-wall, composed of two layers: an outer **circular** and an inner **longitudinal**. The muscles of the body-wall are arranged in segments, corresponding to the external segmentation of the skin. In the circular muscular layer (C.M), the muscle fibres are arranged round the circumference of the body, but in the longitudinal layer (L.M) they are arranged along the long axis of the body.

CHAPTER XI

ORGANS OF CIRCULATION

Crayfish. The blood-vascular system of *Astacus*, like that in the Arthropoda generally, is not a **closed system**, i.e. does not consist of arteries, capillaries, and veins, closed along their whole course, except at their origin from and entrance to the heart. But instead it consists of a central organ, the **heart**, lying dorsally to the alimentary canal, and just beneath the thoracic carapace between the cardio-branchiac grooves (Fig. 63), and from which there proceeds a series of **arteries** that ultimately open into lacunar spaces, situated among the organs

and tissues of the body. From these spaces the blood is collected into a large cavity lying in the endophragmal system, called the **sternal sinus** (Fig. 63, STR.C), whence it passes to the gills to be aërated, and thence, through certain channels (BR-CAR.C) in the thoracic epimera (EP), to the **pericardial sinus** (P), in which the heart lies.

The heart is approximately hexagonal in form, and its walls are strongly muscular (Fig. 68). It is held in position in the pericardial sinus partly by three pairs of fibrous bundles, the **alæ cordis**, and partly by the arteries arising from it. Its walls are perforated by three pairs of apertures, the **ostioles** (OS), of which one pair is situated in the dorsal wall, one pair in the ventral wall, and a single one in either of the two lateral walls: the ostioles are guarded by membranous folds playing the part of valves, which are so arranged that, while blood can pass freely from the pericardium to the cavity of the heart, it cannot pass in the contrary direction. In a similar way the openings of the arteries from the heart are guarded in such a way that the blood flows from the heart to the arteries, but not vice versa.

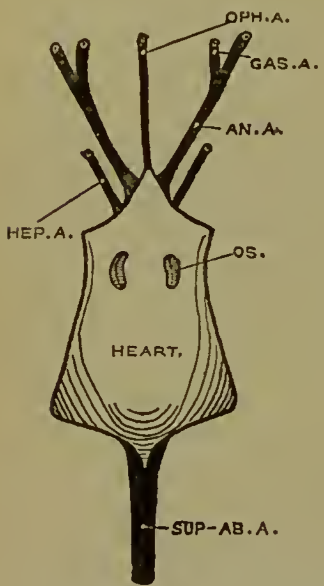


FIG. 68. Dorsal view of heart of *Astacus* (Crayfish). AN.A = antennary artery; GAS.A = gastric artery; HEP.A = hepatic artery; OPH.A = ophthalmic artery; OS = ostiole; SUP-AB.A = supra-abdominal artery (dorsal abdominal artery).

From the middle of the anterior margin of the heart there passes forwards a small median artery, the **ophthalmic artery** (Fig. 68, OPH.A), over the dorsal wall of the stomach to near the rostrum (Fig. 69, O.A), where it divides into two branches, one of which supplies each eye (E). On either side of the ophthalmic artery there arises from the heart an **antennary artery** (Fig. 68, AN.A), which passes forwards and downwards (Fig. 69, A.A) through the substance of the hepato-pancreatic gland (L), and gives off a **gastric artery** to the side-wall of the stomach (C.S, S); thence passing forwards to the anterior end of the head it divides into branches which supply the green gland (G.G), antenna (AN), antennule, rostrum, and certain muscles in this region.

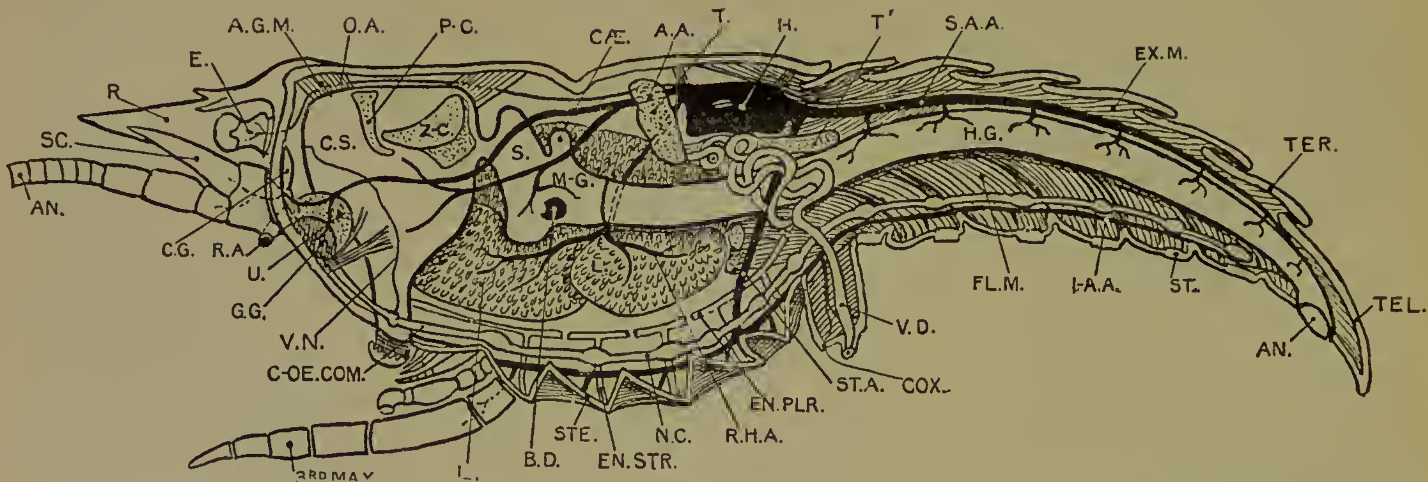


Fig. 69. Median-vertical section of Crayfish (*Astacus*). A.A = antennary artery; AN (to the right) = anus; AN (to the left) = antenna; A.G.M = anterior gastric muscle; B.D = aperture of bile-duct; C.G = cerebral ganglion; CÆ = cæcum; COX = coxopodite of last thoracic appendage; C.S = cardiac portion of stomach; C-Œ.COM = circum-œsophageal commissure; E = eye-stalk; EN.PLR = endo-pleurite; EN.STR = endosternite; EX.M = extensor muscles; FL.M = flexor muscles; G.G = green gland; H = heart; H.G = hind-gut; I-A.A = infra-abdominal artery; L = liver; M-G = mid-gut; N.C = nerve cord; O.A = ophthalmic artery; P-C = ptero-cardiac ossicle; R = rostrum; R.A = renal aperture; R.H.A = right hepatic artery; S = pyloric portion of stomach; S-A.A = supra-abdominal artery (dorsal abdominal artery); ST.A = sternal artery; ST = sternum; STE = sternite; SC = scaphocerite; T = median (anterior) lobe of testis; T′ = paired (posterior) lobes of testis; TER = tergum; TEL = telson; U = ureter; V.N = visceral nerve; V.D = vas deferens; Z-C = zygo-cardiac ossicle; 3rd MAX = third maxillipede. In front of it can be seen the second and first maxillipedes, the second and first maxillæ, and the mandible.

From the ventral surface of the heart and just beneath the antennary arteries there arise two others, one on either side, which pass outwards and downwards to supply the hepato-pancreatic gland ; these are the **hepatic arteries** (Fig. 68, HEP.A & Fig. 69, R.H.A). From the posterior border of the heart, in the middle line, there arises a large **dorsal (superior) abdominal artery** (Fig. 68, SUP-AB.A), which passes backwards to the posterior extremity of the abdomen, and supplies the intestine and muscles of the segments through which it runs (Fig. 69, S-A.A). At the junction of this vessel with the heart (Fig. 69, ST.A) there arises another which passes directly downwards, sometimes to the left and sometimes to the right of the intestine (Fig. 63, S.A & H.G), and piercing the nerve chain between the penultimate and ultimate thoracic ganglia, divides into two; this vessel is the **sternal artery**, and of the two branches which arise from it, one runs forwards (Fig. 69), immediately beneath the nerve cord (N.C), as the **ventral thoracic artery**, supplying the appendages from the mandibles to the last thoracic, and the other passes backwards, as the **ventral (inferior) abdominal artery** (Fig. 69, I-A. A), to supply the muscles and appendages of the abdomen.

All these arteries break up into smaller vessels, and these terminate eventually in blood sinuses, which in their turn ultimately lead into two large sinuses lying in the endophragmal system, on either side of, and including, the sternal canal, and called the **ventral** or **sternal sinuses** (Fig. 63, STR.C). From these the blood passes up along the afferent channels of the gills in a direction indicated by the arrows, thence down along the efferent channels to six canals lying in the thoracic epimeron, called the **branchio-cardiac canals** (Fig. 63, BR-CAR.C & Fig. 64, BR-C.C), and which open at their dorsal extremities into the pericardial sinus (P). It is while the blood is passing through the gills (AR.BR, PO.BR), the walls of which are composed of a thin membrane, that the interchange between the carbon dioxide of the blood and the oxygen of the water takes place.

It will be observed that the gills are here placed in the course of the *returning* blood, and not, as in the dogfish, in the course of the blood just *leaving* the heart; the same statement is true of the mussel. The heart of the crayfish and mussel is, therefore, a **systemic** one, since it propels blood direct to the system ; while that of the dogfish is a **branchial** one. Hence the difference in the nature of the blood in the two cases, i. e. in the latter it is venous blood just returned from

the system, while in the two former it is arterial blood just returned from the respiratory organs.

The cavity in which the viscera lies in *Astacus* is thus a blood-cavity through which the blood circulates; it is not, therefore, a true cœlom or body cavity, like that in the earthworm, dogfish, frog, and rabbit, and it is distinguished by calling it a **hæmocœl.** The pericardium of *Astacus* is not homologous with that of *Anodonta*, frog, dogfish, or rabbit, since it is part of the hæmocœl, and not of the true cœlom as in them.

The blood of the crayfish is colourless, and consists of a clear fluid, in which float innumerable **white corpuscles**, which, when examined in the living condition, may be seen to undergo constant changes of form; their average diameter is about $\frac{1}{1000}$ inch. The liquid portion, or **plasma**, consists of water with a very small percentage of proteid matter in solution. When extracted from the body the blood coagulates, giving rise to a fairly firm clot. This coagulation is the result of the formation of a large number of fibrils formed within the plasma, and which seem to take origin from a number of the corpuscles, since all of them may be seen to radiate, in groups, from various corpuscles. It has been observed that certain of the corpuscles burst at the moment of the extraction of the blood from the body, and it is from these that the fibrils radiate. It is possible that, when the corpuscles disintegrate, they liberate a **ferment** which converts one of the proteids of the plasma into an insoluble, filamentous form, to which the name **fibrin** has been given.

Cockroach. The blood-vascular system of insects is much reduced, and consists of a tubular heart lying dorsally to the alimentary canal, and of a series of irregular spaces or blood sinuses. Of these sinuses there is a larger, dorsal one, partially separated from the other more ventrally situated ones by a series of paired, segmentally arranged, triangular **aliary** muscles, the broad ends of which are attached to the chambers of the heart, while their narrow ends are fastened to the latero-dorsal body-wall. The dorsal sinus, thus incompletely divided off from the others, contains the heart, and receives the blood from all parts of the body; it is called the **pericardial sinus.** The **heart** itself is merely a tube, the lateral walls of which are pierced by paired ostioles arranged inter-segmentally. Just behind each ostiole is an internal membranous fold, so disposed that it allows blood to flow forwards in the direction in which the contractile wave of the heart passes, but not in the reverse direction. The ostioles are also guarded

by membranous valves which let blood pass into the heart, but not outwards. The posterior termination of the heart is closed, but the anterior one is open, and it is through this that the blood, carried into the heart through the lateral ostioles from the pericardium, passes out into the sinuses in the anterior region of the body, whence it travels backwards, and ultimately reaches the pericardial sinus again.

The heart is composed of an external and internal elastic membrane, between which is a layer of muscle fibres, for the most part circularly arranged.

Fresh-water Mussel. The heart consists of three chambers (Figs. 72 & 74), of which the two **auricles** (AU) are lateral and the **ventricle** (V) median in position. It lies in a large, well-defined **pericardium** (P), immediately above the organ of Bojanus (R.O). The pericardium is the only representative of the cœlom: at its anterior angle (Fig. 74, R-P.A.) it is perforated by two apertures, one on either side, called the **reno-pericardial apertures**, and which communicate with the two renal organs (U); and posteriorly its lateral walls are thickened by a brown, glandular patch, the **organ of Keber**, which is of the nature of a pericardial gland and is probably excretory in function.

The auricles of the heart (Fig. 74, AU) are two thin-walled, triangular sacs, attached by their bases to the lateral margins of the floor of the pericardium, and opening by their apices, each into a lateral aperture, on either side, in the wall of the ventricle. When fully distended, the latter is a somewhat oblong-shaped organ, the walls of which are muscular and elastic, and capable of both great distension and contraction. It is perforated throughout its length by the rectum (Fig. 72, R), so that its cavity is more or less a cylindrical one, surrounding the rectal tube. There arise two arteries from it, an **anterior** (Fig. 72, ANT. A) and a **posterior aorta** (POS. A), of which the latter passes beneath the rectum and runs backwards as far as the posterior adductor muscle (P.A), where it divides into three main branches, which supply the rectal wall, the adductor and protractor muscles, the posterior ends of the gills, and the mantle (P). The anterior aorta runs forward above the rectum, through the liver substance (L) to near the anterior adductor muscle (A.A), where it divides into a **pedal** and a **visceral branch**, of which the former supplies the anterior adductor and retractor muscles, the mantle, the labial palps, the body-wall and the muscular tissue of the foot; the

latter breaks up into several branches and supplies the wall of the intestine and the gonad (G).

The two arteries which supply either mantle lobe (P) run in its ventral margin and form an anastomosis; from the principal vessel (**pallial artery**) thus formed there is given off a large number of smaller vessels which break up into more or less lacunar spaces in the tissue of the mantle. These by their convergence again form a series of definite, small channels, all of which open into the **pallial vein**, that skirts the ventral margin of the mantle, and which at either end turns upwards and enters the **efferent branchial vein**; this latter runs along the dorsal margin of the outer lamella of the outer gill (O.G), and at once returns the blood to the auricle of the heart of the same side of the body.

All the branches derived from the two aortæ ultimately open into lacunar spaces among the tissues of the body (Pl. II, Fig. 2); these lacunæ are in communication with several venous vessels situated in the dorsal portion of the visceral mass, and which by their convergence form a single, median vein, the **vena cava**, that lies immediately beneath the pericardium and between the two organs of Bojanus. At its posterior end, the vena cava receives one or two small venous vessels, bringing back the blood from the posterior adductor and posterior retractor muscles. From both sides of the vena cava there is given off along its length a series of small veins (**afferent renal**), which pass to the glandular portion of either organ of Bojanus, and break up in its substance into a capillary meshwork. The factors of this meshwork open into four veins, the **efferent renal veins**, which converge towards the hinder third of the gills, and open into a longitudinal vessel, the **afferent branchial trunk**, which runs the whole length of them, along the plane of coalescence of the outer with the inner gill. From this trunk there is given off a number of vessels, one set of which passes down in the substance of the inner lamella of the outer gill (Fig. 72, O.G), and the other in the substance of the outer lamella of the inner gill (I.G); these vessels are the **afferent branchial vessels**. Each afferent vessel gives off a number of small vessels which pass across the inter-lamellar space, and open into the **efferent branchial vessels**, which in the outer gill are situated in the outer lamella, and in the inner gill, in the inner lamella. The efferent branchial vessels of both gills open into a longitudinal trunk, the **efferent branchial trunk**, which runs along the length of the dorsal margin of the outer lamella of the outer gill of either side. This trunk

also receives the **pallial vein** and those coming from the organ of Keber. It then opens by several short vessels into the auricle of the heart of the corresponding side of the body.

The course of the blood is, therefore, as follows: from the ventricle of the heart it is propelled through the two aortæ to the lacunæ or blood sinuses (Pl. 2, Fig. 2), thus bathing all the tissues of the body, including the mantle; from the sinuses it is returned through a few venous vessels, chiefly situated in the visceral mass, to the vena cava; from this it passes through the organs of Bojanus, which excrete from them its nitrogenous waste; thence it travels through the substance of the gills, where it takes up oxygen from, and gives up carbon dioxide to the water bathing them. Thus rid of the nitrogenous and carbonaceous waste materials, and freshly oxidized, it is the purest blood in the body; in this condition it is at once carried to the auricles of the heart and thence back again to the ventricle.

It will be seen that in any given cycle of the circulation, the whole of the blood, with the exception of that small portion which passes through the mantle, must pass through both the renal and respiratory organs before returning to the heart. This is the very reverse of that in the crayfish (Pl. 2, Fig. 1), where only a comparatively small proportion of the whole blood passes through the renal organ (green gland) in any one cycle. It must, however, be borne in mind, that in the crayfish, other tissues, such as the skin, may probably perform a renal function. In the dogfish and frog, roughly nearly one half of the blood passes through the renal organ in any given cycle, while in the rabbit only a fraction of the whole does so. In *Amphioxus*, owing to the situation of the nephridial tubules on the branchial bars, the whole of the blood must pass both through them and the respiratory organs in any given cycle of the circulation. The same is true of the earthworm, for all the blood passes through the renal organs, in every cycle of the circulation.

Earthworm. The organ in the earthworm which corresponds to the heart of the Crustacea (crayfish) and Insecta (cockroach) is a contractile, tubular vessel lying along the dorsal surface of the intestine (Fig. 71, SP.V) in the mid-line, and extending from end to end of the body; it is called the **supra-intestinal vessel**. Anteriorly it breaks up into several small vessels that spread out in the wall of the pharynx and buccal sac. It can be seen in a living worm, preferably a small one, lying beneath the skin, rhythmically contracting in such a way that a contractile wave passes along it from its posterior to its anterior

end; the waves of contraction follow each at a rate, such that, before the first has reached the anterior end of the vessel, the second has commenced at the posterior. The blood is, therefore, driven from behind forwards.

Anteriorly there arise from the supra-intestinal vessel five pairs of lateral, contractile, tubular organs, situated on either side of the œsophagus in segments seven to eleven. These are called **pseudo-hearts** (H), and open beneath the œsophagus into a median vessel, the **supra-neural vessel** (Fig. 76), which runs the entire length of the body, suspended in a fold of peritoneum, just dorsal to the nerve cord (N.C). Anteriorly and posteriorly this vessel branches, and its branches are so arranged, with respect to those of the supra-intestinal on the pharyngeal and buccal walls, as to suggest an anastomosis between the two.

Lying in the sheath of the nerve cord (N.C), and running throughout its length, are three vessels, one situated in the mid-ventral line, and the other two, one on either side; these are known, respectively, as the **sub-neural** and **lateral neural vessels**. They are somewhat indistinctly represented in the figure.

Situated in the middle line, running the whole length of the ventral surface of the alimentary canal, and partially embedded in the investing chloragogen cell mass, is a small vessel, the **sub-intestinal vessel**, in communication with the supra-neural by means of a series of small median vessels.

There are thus four median vessels extending the whole length of the worm, one above and below the alimentary canal, and one above and below the nerve cord. In addition to these median vessels and the lateral pseudo-hearts there are certain other lateral vessels which serve to place in communication with one another the four vessels just described. They are a pair of **lateral œsophageal** (Fig. 71) arising from the supra-intestinal vessel in the fifteenth segment, and passing forward along the side-walls of the œsophagus, which they supply, as well as the calciferous glands and the lateral wall of the pharynx. In every segment of the intestinal region a pair of **lateral intestinal vessels** arise on either side from the supra-intestinal vessel, and in the wall of the intestine break up into capillaries which anastomose with a series of small vessels that open into the sub-intestinal vessel. In every segment of the body, the first few anterior ones excepted, there arises from the supra-neural vessel a pair of **nephridial arteries** which pass through the circumneural arcade to

reach the glandular portion of the nephridial tubes in the segment next behind, upon the surface of which they break up into capillaries, and which by their convergence ultimately form the **nephridial veins** that open into the sub-neural vessel. The sub-neural and supra-intestinal vessels are placed in communication with one another in every segment of the body by a pair of vessels, the **circular blood-vascular commissures**, that give to, and receive from, the body-wall a number of small vessels which are in connexion with a plexus of capillaries, some of which lie between the epidermal cells. The lateral neural vessels are in communication with the sub-neural vessel by means of a pair of inter-neural vessels in each segment of the body.

The course of the blood through the vessels will, therefore, be as follows (Pl. II, Fig. 3): from the supra-intestinal it passes through the pseudo-hearts to the supra-neural, and from the same vessel it passes through the lateral intestinal vessels to the sub-intestinal, thence to the supra-neural; anteriorly the blood, which is carried forwards beyond the first pseudo-heart, and also through the lateral œsophageal vessel, finds its way to the supra-neural by means of the anastomosis which exists between these three vessels on the pharyngeal walls. From the supra-neural all the blood must pass through the nephridial arteries and veins to the sub-neural, and from this it is carried to the muscles and skin, and thence back to the supra-intestinal by means of the circular blood-vascular commissures.

While the blood is passing through the capillaries derived from the nephridial arteries it is deprived of its nitrogenous waste, and of its carbonaceous waste while passing through the capillaries of the skin, where also it becomes oxygenated.

The blood of *Lumbricus* consists of a red fluid, the colour of which is due to dissolved **hæmoglobin**, in which are immersed a number of very small oval corpuscles, with minute nuclei. The corpuscles that resemble the white corpuscles of other animals are to be found, not in the blood, but in a fluid contained in the cœlom and called the **perivisceral cœlomic fluid** (Fig. 76, C.C).

Compared to the blood system of *Astacus*, *Anodonta*, and *Periplaneta*, that of *Lumbricus* is distinguished by the fact that it is a closed system, i.e. the blood is contained in a closed series of vessels and capillaries, or, in other words, the blood is not discharged into open lacunæ; it is further contrasted by the presence of hæmoglobin, which is contained, not in the red corpuscles as in Vertebrates, but in the plasma or liquid portion of the blood.

THE BLOOD-VASCULAR SYSTEM OF ASTACUS, PERIPLANETA, ANODONTA, AND LUMBRICUS CONTRASTED AND COMPARED.

Astacus and Periplaneta.	Anodonta.	Lumbricus.
1. Heart is systemic.	Heart is systemic.	Heart is systemic.
2. Heart is single-chambered and shortened : in *Periplaneta* it is tubular and elongated.	Heart consists of a ventricle and two auricles.	Heart is tubular and extends the body length.
3. Pericardium a hæmocœl.	Pericardium a portion of cœlom.	A definite pericardium not formed.
4. Vascular system is open.	Vascular system is open.	Vascular system is closed.
5. In any one cycle, only a portion of the blood passes through the renal organ.	In every cycle the whole of the blood passes through the renal organ.	In every cycle the whole of the blood passes through the renal organs.

CHAPTER XII

THE ENTERIC OR ALIMENTARY CANAL

The Crayfish. The alimentary canal may be divided into three portions, which are ontogenetically distinct: the **fore-gut, mid-gut,** and **hind-gut.** Of these the mid-gut alone is of endodermal (hypoblastic) origin, the other two arising as invaginations of the embryonic ectoderm, i. e. the **stomodæal** and **proctodæal invaginations** respectively. In the crayfish the mid-gut is exceedingly short, but in other Crustacea (*Entomostraca*) it forms the longest portion of the alimentary tract. The internal surface (morphologically the outer) of the fore-gut and the hind-gut is lined with a chitinous cuticle continuous with that of the exoskeleton, and, like that, certain portions of it in the fore-gut are calcified.

Fore-gut. This opens from the mouth by a short tube, the **œsophagus** (Fig. 69), which passes through the circum-œsophageal commissures (C-OE. COM), and enters a spacious sac that almost entirely fills the cavity of the cephalic portion of the cephalo-thorax. This sac, the **stomach** (C.S and S), is divisible into a larger anterior

portion, the **cardiac division** (C.S), and a smaller posterior, the **pyloric division** (S). These two divisions are clearly marked off from each other by two constrictions, one in the dorsal wall and the other, forming the **median cardio-pyloric valve**, in the ventral wall. In the lateral wall, in front of the median valve and immediately behind the opening of the œsophagus, there is on either side another fold bearing long hairs, the **lateral cardio-pyloric valve**, and which, like the median valve, does not extend more than half way towards the dorsal surface, so that, in the ventral portion of the cardiac division, the cavity of the stomach is reduced to a slit-like aperture. Dorsally, the wide aperture is guarded by an arrangement of calcified bars, some of which bear teeth-like bodies, and which collectively are termed the **gastric mill**. The stoutest of these calcified bars or ossicles, the **cardiac ossicle**, is situated in the dorsal wall of the cardiac division, and stretches transversely across almost its entire breadth (Fig. 70, A & C, C). In the middle line its hinder margin articulates with another ossicle, the **uro-cardiac ossicle** (UC), which lies in the front wall of the dorsal constriction that divides the stomach into two parts, and which bears at its ventral, free extremity the conical **median tooth** (M.T). In the dorsal wall of the pyloric division of the stomach there is situated the **pyloric ossicle** (P), the front margin of which articulates with the **pre-pyloric ossicle** (P.R) that lies in the hinder wall of the dorsal constriction; the ventral, free extremity of this articulates with the hinder surface of the corresponding

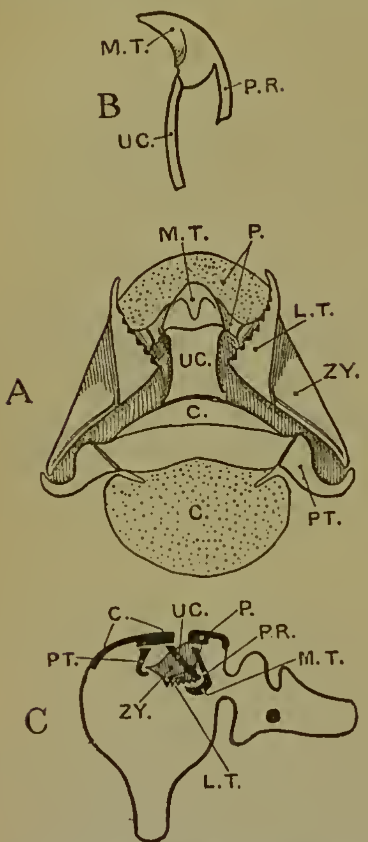


FIG. 70. The gastric mill of the Crayfish (*Astacus*). A. The stomach wall has been cut open along the mid-ventral line and its lateral walls laid flat, giving an internal view of the mill. B. The median tooth and its ossicles removed and seen from the side. C. A diagrammatic representation of a median-vertical section of the stomach. C = cardiac ossicle; L.T = lateral tooth; M.T = median tooth; P = pyloric ossicle; P.R = pre-pyloric ossicle; PT = ptero-cardiac ossicle; UC = uro-cardiac ossicle; ZY = zygo-cardiac ossicle.

part of the uro-cardiac ossicle. In the lateral walls of the stomach are two pairs of ossicles, the **ptero-cardiac** (PT) and **zygo-cardiac ossicles** (ZY). The former articulate dorsally one with each of the lateral margins of the cardiac ossicle, while ventrally they have the form of a recurved hook, with which the antero-ventral extremity of the zygo-cardiac ossicle articulates. The latter is somewhat triangular in form, and in part articulates with an antero-lateral projection of the pyloric ossicle and in part with the recurved hook of the ptero-cardiac. Upon its inner surface and just behind its articulation with the ptero-cardiac it bears a serrated tooth, the **lateral tooth** (L.T).

This complex apparatus is moved by several muscles, the two most important of which are the paired **anterior** and **posterior gastric muscles** (Fig. 69, A.G.M). The former arise from the procephalic processes, which are chitinous projections within the cephalic carapace at the root of the rostrum, and are inserted into the dorsal surface of the cardiac ossicle. The posterior gastric muscles arise from the internal surface of the cephalic carapace immediately in front of the cephalic groove (Fig. 69) and are inserted into the dorsal surface of the pyloric ossicle. The action of these two muscles is to pull the cardiac and pyloric ossicles apart, the final effect of which, when modified by other muscles situated in the lateral wall of the stomach which control the lateral ossicles, is to bring the median tooth downwards and forwards and the lateral teeth inwards and backwards, so that the three meet together. The cardiac and pyloric ossicles are brought nearer to one another again and the three teeth thus separated, mainly by the contraction of a pair of muscles passing between the two ossicles, and called the **cardio-pyloric muscles.**

The student can easily observe the working of the gastric mill for himself by the following means: remove the stomach from the body and by a ventral, median incision lay it open. Cut away with scissors some of the ventral wall on either side of the incision so as to clearly reveal most of the ossicles and the three teeth. Then seizing hold of the posterior and anterior extremities of the stomach by two pairs of forceps, imitate the action of the gastric muscles by alternately pulling the two extremities apart and allowing them to approach again. When pulled apart the three teeth will meet, and when allowed to approach the teeth will separate.

Internally the lateral walls of the pyloric division contain three pairs of folds bearing hairs, and which serve to finally filter off any coarse particles that may have passed the gastric mill.

The demarcation between the pyloric portion of the stomach and the mid-gut is clearly marked by the abrupt ending of the chitinous layer of the former, which dorsally is terminated by a valve-like projection, and beneath which is the opening of the **hepato-pancreatic** or **bile duct** (Fig. 69, B.D).

In the lateral wall of the cardiac division of the stomach there is developed during the summer season only a round, plate-like calcareous concretion called the **gastrolith**, which at the periodical shedding of the calcified exoskeleton, is liberated into the stomach, ground to powder and absorbed with the food. It probably supplies part of the material out of which the new exoskeleton is formed.

The **mid-gut** (Fig. 69, M-G) is very thin walled, not more than a quarter of an inch in length, and dorsally, at its junction with the pyloric portion of the stomach, is prolonged into a blind sac-like outgrowth, the **cæcum** (CAE). Its epithelium is differently constituted from that lining the fore- or hind-guts, and there is no chitinous layer. At its anterior end it is perforated on either side by the apertures of the hepato-pancreatic ducts, which arise in the course of development as evaginations of its wall.

The **hepato-pancreatic gland** (Fig. 69, L) is a tubular organ, the tubules of which are arranged around and open into the hepato-pancreatic duct, which consists of two tubes united at their origin from the mid-gut, and one of which runs forwards and the other backwards. The tubules which form the mass of the gland are very numerous and fill a great part of the cephalo-thorax; they are arranged on each side into three lobes: an anterior, a lateral, and a posterior. Examined microscopically, two sorts of cells may be distinguished forming the epithelium of the tubules: **ferment cells**, whose secretions digest fibrine and other proteids, and **hepatic cells**, whose fatty secretion contains a colouring matter allied to the bile-pigment of Vertebrates. The gland is therefore digestive, like the Vertebrate pancreas, and excretory, like the Vertebrate liver; hence it must be called a hepato-pancreatic gland and not simply a liver.

The **hind-gut** (Figs. 63 & 69, H-G) is in the crayfish very long, extending from the mid-gut which lies beneath the cephalic groove to the last segment of the abdomen, upon the ventral surface of which it opens by the anal aperture (AN). Its wall is thick, and thrown into a series of longitudinal folds, and the whole is covered internally by a chitinous cuticle of the same nature as that lining the fore-gut.

Cockroach. Like that of the crayfish, the alimentary canal of the

cockroach consists of a **fore-gut** derived from the stomodæal invagination, of a **mid-gut** derived from the **mesenteron**, and of a **hind-gut** derived from the proctodæal invagination.

Fore-gut. The mouth is situated at the ventral surface of the head between the mandibles, and passes backwards into a short **buccal cavity**, the posterior wall of which is thickened to form the **lingua** or tongue. The **œsophagus** leading from the buccal cavity, is a long narrow tube which, gradually dilating in size, passes into a large pyriform sac, the **crop**, that extends back far into the abdomen. Its walls are extensible and muscular. At its posterior end it opens into a conical, thick-walled, markedly muscular sac, the **gizzard**, the limit between the cavity of which and that of the crop is indicated by a series of papilla-like projections. The internal surface of the gizzard is covered with a cuticular layer composed of chitin, which projects into the cavity in the form of six blade-like folds the free margins of which are serrated; they thus form six cutting teeth. Behind these there are six small elevations bearing hair-like setæ. The apex of the conical gizzard is joined to the **chyle-stomach**, and the cuticular lining of the former projects backwards into the cavity of the latter for a little distance, in the form of a funnel-like tube.

The **salivary glands** and **receptacles** are situated on either side of the œsophagus; they arise as invaginations of the oral lip of the stomodæum. The salivary glands are paired on either side, and from each gland a duct runs forwards which very shortly unites to form a single duct on either side; these passing forwards unite beneath the nerve cord to form a single median duct, that opens to the exterior, in the neighbourhood of the mouth behind the lingua. The salivary receptacles or vesicles lie between the glands and the wall of the œsophagus, and are single pyriform sacs on either side; the ducts proceeding from the two receptacles unite beneath the nerve cord, in the middle line, to form a single duct, which passing forwards, enters the median duct of the salivary gland at the bend of the neck.

Mid-gut. The **chyle-stomach**, or as it is sometimes called, the **mesenteron**, is a tube of uniform diameter, the internal surface of which is lined with a columnar epithelium, which is concerned with the digestion and absorption of the food material; it is not, therefore, lined with a chitinous cuticle. At its anterior end where it joins the gizzard, it receives seven or eight club-shaped glands, called the **hepatic cæca**; these arise as diverticula of the anterior portion of the embryonic mesenteron, and are therefore homologous with the

hepato-pancreatic gland of the crayfish and the hepatic gland of the mussel, which arise in the same manner. The hepatic cæca pour into the mesenteron a digestive fluid which is mixed with the food at this point.

Hind-gut. At its posterior end, the chyle-stomach or mesenteron passes into a shorter and narrower tube, the **intestine** or **ileum**, and which, like the stomach, is concerned with the digestion and absorption of food. At the junction of the two parts, there is a row of very numerous thread-like tubules, arranged round the circumference of the ileum ; these are the **Malpighian tubules**, and they arise as diverticula of the front portion of the **hind-gut**. They are probably excretory in nature, since coloured concretions containing uric acid are found in their epithelial cells.

The ileum opens into a much wider tube, the **colon**, the cavity of which is lined by a delicate chitinous cuticle. Posteriorly the colon opens into a wide, short tube, the **rectum**, the cavity of which is lined with the same material as that of the colon, and which is thrown into six longitudinal ridges. The rectum opens between the podical plates by the **anal aperture**.

Earthworm. Like that of the crayfish, the alimentary canal of the earthworm can be divided into three regions, according to their ontogenetic origin : the **fore-gut**, the **mid-gut**, and the **hind-gut**. The fore- and hind-guts are ectodermal invaginations, but the mid-gut is of endodermal origin and arises from the archenteron (mesenteron) of the gastrula stage. In the adult the fore-gut consists of the **buccal cavity** and **pharynx** (Fig. 71, BS & PH), and the hind-gut is represented by a very short portion of the termination of the intestine which opens to the exterior by the anus. The mid-gut, in marked distinction to that in the crayfish and the cockroach, forms by far the greater portion of the canal, and in the adult consists of **œsophagus** (O), **crop** (C), **gizzard** (G), and **intestine** (I).

Fore-gut. The mouth is an aperture in the middle of the ventral surface of the first segment, the anterior portion of which projects beyond the mouth as the **prostomium**, while the part immediately behind, the **peristomium**, is slightly constricted off from the remainder of the segment by a shallow groove. The mouth leads into a thin-walled sac occupying the greater part of the first three segments of the body, the **buccal sac** (Fig. 71, B.S), which is separated from the thick-walled **pharynx** (PH) behind by a somewhat pronounced constriction. The **pharynx** occupies the next three segments of the body, and its

dorsal wall is very muscular, much thickened, and thrown into two sucker-like folds. It is connected to the body-wall by a large number of muscle fibres (PH.M), the pharyngeal muscles.

Mid-gut. The pharynx passes into a tubular organ, the **œsophagus** (O), which extends back as far as the fourteenth segment, when it becomes dilated to form a distensible sac, the **crop** (C), which reaches to the seventeenth segment. In the eleventh segment two pairs of lateral pouches open into the œsophagus, and there is also a similar pair in the twelfth segment; the three pairs are very richly supplied with blood-vessels, and at certain seasons of the year they are filled with calcareous concretions of unknown significance. They are called **Morren's, œsophageal,** or **calciferous glands.** The crop passes into the **gizzard** (G), a very thick-walled muscular organ, lined internally with a thick cuticle, and extending from segments seventeen to twenty. At its junction with the intestine, its wall projects inwards in the form of a ring-like fold, which is directed forwards, and serves as a valve, preventing the backward passage

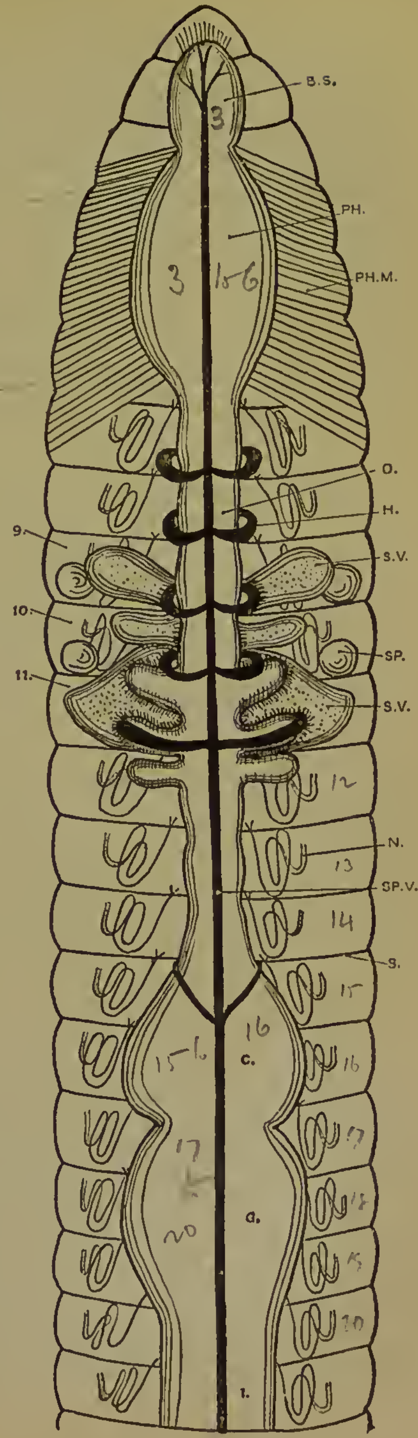


FIG. 71. Dorsal dissection of Earthworm (*Lumbricus*), to show alimentary canal, the position of the nephridia, and certain parts of the reproductive and vascular systems. B.S = buccal sac; C = crop; G = gizzard; H = pseudo-hearts; I = intestine; N = nephridia; PH = pharynx; PH.M = pharyngeal muscles; O = œsophagus; S = septa dividing the cœlomic cavity into segments; SP = spermathecæ (seminal receptacles); S.V = vesiculæ seminales; SP.V = supra-intestinal blood-vessel; 9, 10, 11 = the ninth, tenth, and eleventh segments.

of the food until it has been sufficiently triturated by the action of the gizzard.

The **intestine** (I) is a uniform tube leading from the gizzard to the very short rectum in the last segment of the body. Its dorsal wall (Fig. 76, TY) is folded inwards as a longitudinal ridge along its whole length, forming the **typhlosolis**, the object of which is to increase the absorptive surface of the intestine without increasing the space that it occupies. Externally the surface of the intestine is covered by a thin layer of yellowish-brown material, formerly called the hepatic substance, because it was supposed to act the part of a liver ; but it is now known that it has no connexion with the lumen of the gut, and is rather intimately connected with the blood-vessels, and therefore probably excretory in nature. It consists of modified cells derived from the peritoneum lining the body cavity, and very often may be found surrounding, more or less completely, nearly all the blood-vessels in the body. They are known as **chloragogen cells** (Fig. 76, CL.C). Their brown colour is due to pigment granules which they have taken from the blood-stream, not in the form of granules, but as some other material which their activity converts into granules, and which will be discharged by them into the body cavity, whence the granules will find their way to the exterior through the nephridia (N).

Hind-gut. This is a very short portion of the posterior extremity of the intestine that opens to the exterior by the anus. It is that part of the intestine lying between the anus and the termination of the typhlosolis, and is contained in the last body segment.

Fresh-water Mussel. As in the earthworm, the greater length of the intestinal tract is derived from the archenteron (mesenteron), and is of endodermal (hypoblastic) origin. The fore-gut, represented by the œsophagus, is very short, and the hind-gut or rectum is relatively long, and is characterized by the fact that it pierces the ventricle of the heart.

Fore-gut. Owing to the absence of the cephalic portion of the body, there is no buccal mass or pharynx as in other Mollusca, and the **œsophagus** (Fig. 72, Œ), which lies just behind the anterior adductor muscle (A.A), is very short, and somewhat suddenly dilates to enter the **stomach** (S). Anteriorly the œsophagus opens by a small aperture, the mouth, into the infra-branchial chamber (I.B.C) ; and on either side of the mouth are two triangular folds of skin, the **labial palps**.

Mid-gut. The stomach (S) is the most anterior portion of this, and is a somewhat rounded sac receiving the two bile-ducts (B.D) on

either side, a little behind the point where the œsophagus joins it. The **digestive gland** (L) lies on either side of the stomach, and is a richly branched, tubular gland, the epithelium lining which contains three kinds of cells: **hepatic, ferment,** and **calcareous cells.** The stomach leads posteriorly into the **intestine** (IN), which forms three U-shaped loops in the substance of the laterally compressed body; throughout its length the intestine is traversed by an infolding of its

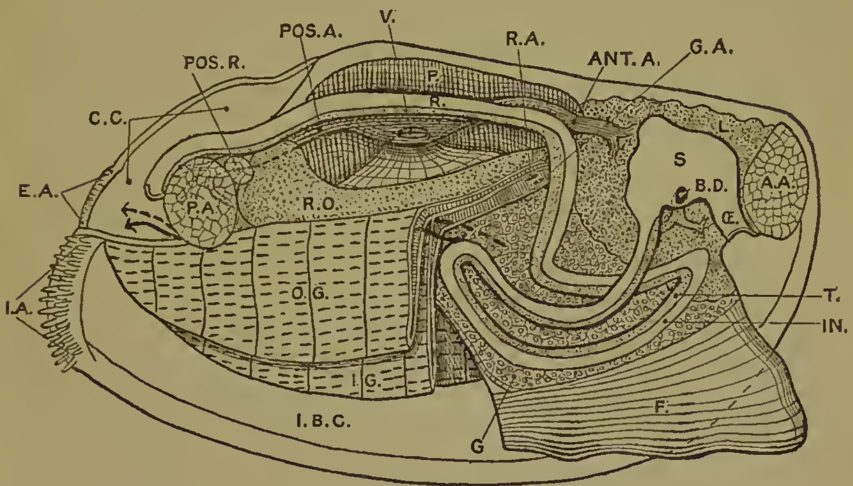


FIG. 72. Side dissection of the Fresh-water Mussel (*Anodonta*), showing the alimentary canal, the pericardium, heart, relation of the gills, and the renal and hepatic organs. A.A = anterior adductor muscle; ANT.A = anterior aorta; B.D = bile duct; C.C = cloacal chamber; E.A = exhalent aperture; F = foot; G = gonad; G.A = gonadial (genital) aperture; I.A = inhalent aperture; I.B.C = infra-branchial chamber; I.G = inner gill; IN = intestine; L = liver; O.G = outer gill; Œ = œsophagus; P.A = posterior adductor; POS.A = posterior aorta; POS.R = posterior retractor; P = pericardium; R = rectum; R.A = renal (nephridial) aperture; R.O = renal organ (organ of Bojanus); S = stomach; T = typhlosolis; V = ventricle. The continuous arrow is inserted in the supra-branchial chamber of the outer gill, and the broken arrow in that of the inner gill.

wall, forming a **typhlosolis** (T). Turning upwards the intestine reaches the pericardial cavity (P), when it passes into the rectum.

Hind-gut. The rectum passes through the pericardium and the substance of the ventricle (V) of the heart and over the posterior surface of the posterior adductor muscle (P.A), where it terminates by the anal aperture in the cloacal chamber (C.C).

The whole length of the alimentary canal is lined with columnar ciliated epithelium.

CHAPTER XIII

NERVOUS SYSTEM

THE nervous system of the Invertebrata is characterized by its ventral position, its solid nature—it is not a hollow tube—and by its paired arrangement. Its ventral position is not universal, for among the Nemertine worms the two nerve cords are lateral in position, and in *Balanoglossus* one is ventral but the other dorsal. In the flat-worms the nervous system consists of a plexus of nerve fibres and cells arranged beneath the muscular layer of the body, and which by convergence produce a number of principal nerves, usually six in number, of which two are dorsal, two are lateral, and two ventral. But the flat-worms are lowly Invertebrates, and the diffuseness of their nervous system suggests the condition of that of the higher Hydrozoa, while the formation of principal nerves and a brain foreshadows that of the higher worms; they are thus on the border line between the diffuse nervous system of the Hydrozoa and the concentrated condition met with in most of the higher Invertebrata.

The two lateral nerve cords of the Nemertine worms are unganglionated, that is, they are uniform in size and do not bear enlargements called ganglia at recurring intervals. But everywhere throughout their length ganglion cells may be observed, and since ganglia are but aggregates of ganglion cells, we may imagine that the slightly ganglioniated nerve cord of the earthworm, and the very distinctly ganglionated one of the crayfish, arose from an unganglionated cord like that of the Nemertines by the concentration of the ganglion cells at points where nerves left the cord. The ventral position of the nerve cord of these two animals, in the mid-ventral line, may be explained by supposing that the lateral cords of the Nemertines shifted ventrally until they became apposed in the middle line.

Crayfish. The nervous system of the crayfish studied by itself, without reference to that of other crustaceans, is almost a meaningless structure; and certainly it could not reveal that morphological interpretation of the real nature of the cephalo-thorax that it is enabled to do when compared on the one hand with the nervous system of a more primitive crustacean, and on the other with that of a more specialized one.

We shall therefore study first the essential facts of the nervous

system of *Apseudes*, as illustrating a somewhat primitive condition, and subsequently compare that of the crayfish with it, when we shall then be in a position to judge of the lines of morphological advance along which that of the latter has advanced.

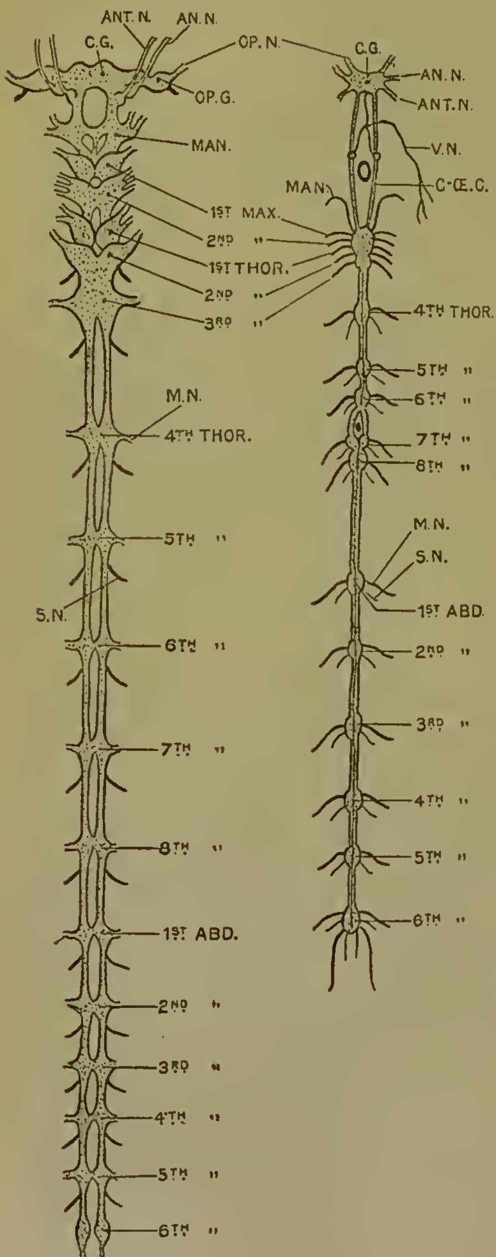
Apseudes is a crustacean in which only two of the eight thoracic segments of the body have become fused with each other and with the head, the remaining six retaining their primitive segmentation; it thus differs in a very marked feature from the crayfish, in which all the eight segments of the thorax are fused with each other and with the head.

The nervous system has also retained the primitive segmentation, for a glance at Fig. 73, left hand, will show that it consists of a **cerebral ganglion** (C.G) lying in front of the œsophagus, and proceeding from it, two distinct nerve chains bearing ganglia, metamerically arranged, and equalling in the number of pairs the number of segments of the body. The first portion of the chain leaving the cerebral ganglion passes round the œsophagus, and is known as the **circum-œsophageal commissure** (C-Œ.C); behind the œsophagus it bears two ganglia (MAN), one on either side, connected by a **transverse commissure**; the nerves proceeding from these supply the mandibles. Behind this pair of ganglia, there are five others (1st & 2nd MAX; 1st to 3rd THOR) distinct from each other, except that they are connected by very short **longitudinal commissures**, and the two ganglia of each pair are just merged with each other in the middle line; these ganglia supply respectively the first and second pairs of maxillæ and the first, second, and third pairs of maxillipedes. There is thus one pair of ganglia for each pair of appendages, or in other words, there is one pair of ganglia for each body segment.

Behind the ganglia which supply the third pair of maxillipedes, there are another eleven pairs, five of which supply the remaining thoracic appendages (4th to 8th THOR), and the other six the appendages of the abdomen (1st to 6th ABD); the first of these eleven are separated from that supplying the third maxillipedes by a long longitudinal commissure, and the same arrangement is true of all the ganglia behind it. Along the whole length of the nervous system, the two longitudinal commissures are distinctly separated from each other, except at the ganglionic enlargements where they are connected by the short transverse commissures.

The nervous system of *Apseudes* thus consists of two chains distinct from each other, each chain bearing ganglionic enlargements,

which are also separate from each other, and so arranged that there is one pair for each segment of the body.



The cerebral ganglion is an exception to this general statement, for as already mentioned *three* pairs of nerves (ANT.N, AN.N & OP.N) pass out from it, but very careful examination shows that each of these arises from a small ganglionic swelling, closely attached to the ganglion.

When we compare the nervous system of *Astacus* (Fig. 73, right hand) with that of *Apseudes*, we find the cerebral ganglion no longer shows evidence of its paired nature, other than by its paired nerves, for instead of being, as in *Apseudes*, a bilobed mass it is more or less rounded. The nerves proceeding from it are the same as those

FIG. 73. The left-hand figure represents the nervous system of *Apseudes* and the right-hand one that of *Astacus* (Crayfish). The cepbalic portion and part of the thoracic of *Apseudes* are based upon figures by Claus. AN.N = antennulary nerve; ANT.N = antennary nerve; C.G = cerebral ganglion; C-Œ.C = circum-œsophageal commissure; MAN = ganglia and nerves supplying mandibles; M.N = motor nerve; OP.G = optic ganglion; OP.N = optic nerve; S.N = sensory nerve; 1st–2nd MAX = ganglia and nerves supplying first and second maxillæ; 1st–8th THOR = ganglia and nerves supplying first to eighth thoracic appendages and segments; 1st to 6th ABD = ganglia and nerves supplying first to sixth abdominal segments and appendages.

leaving the cerebral ganglion of *Apseudes*, and obviously the ganglion is similar in either case, but in *Astacus* the **optic, antennary,** and **antennulary ganglia** have completely merged with the cerebral ganglion.

Passing round the œsophagus from the cerebral ganglion there is an **œsophageal commissure** (C-Œ.C) which unites behind in an ovoidal mass, the **sub-œsophageal ganglion**, from which *five* pairs of nerves pass out; these supply respectively the mandibles (MAN), the first and second pairs of maxillæ (1st & 2nd MAX), and the first and second pairs of maxillipedes (1st & 2nd THOR). Obviously this ovoidal ganglion, larger than any of the others, is not a simple one, but represents the confluence of five pairs of ganglia, which correspond to the first five pairs behind the œsophagus in *Apseudes*. That such a concentration of the nervous system is in reality taking place, is evident by the fact that there lies immediately behind the large ovoidal sub-œsophageal ganglion another which is just beginning to fuse with it, and the nerves from which supply the third pair of maxillipedes (3rd THOR). Behind this, in the thorax, there are five other unpaired ganglia (4th to 8th THOR), connected with each other by a longitudinal commissure, which is single except between two of the ganglia (6th & 7th), where it is double; through the loop which is thus formed the sternal artery passes. The first three of these ganglia (4th, 5th, & 6th) are equidistant from each other, but the fourth and fifth (7th & 8th) are closely approximated and tend to fuse together.

Behind the last thoracic ganglion there are six others situated in the abdomen, connected by a single longitudinal commissure; the last (6th) of these is larger than the others, and from it, not only are nerves given off to the segment in which it lies, but also to the imperfect segment which lies behind.

Continuing the comparison between the two nervous systems, it becomes evident that the confluence of ganglia and commissures which is so marked a feature in the head region of *Astacus*, has also taken place along the whole length of its nerve chain, for the primitively paired ganglia and longitudinal commissures are now single, except at the point where the sternal artery passes through, and where obviously confluence of the commissures could not take place without an alteration in the position of the artery.

The origin of nerves from the last abdominal ganglion, in greater number than those supplying the segment in which it lies, and the

backward trend of these to the vestigial segment next behind, indicate that the ganglion is composed of two ganglia fused together, i.e. that of the 6th and 7th abdominal segments; the vestigial condition of this latter also indicates that the abdomen is in the course of shortening.

If the concentration of the nervous system of *Astacus* is a morphological reality, it may be logically asked whether this concentration has reached a greater development in any other crustacean. The existence of such a condition would demonstrate the logical completeness of the morphological argument, though it is by no means essential for its proof. Among crabs, we meet with such a great concentration of the nervous system, that it is possible to conceive of only one stage further, for in them *all* the ganglia behind the œsophageal commissure have merged into a single one lying in the thorax, and from which nerves pass out to supply the mandibles and all the appendages behind.

In *Astacus*, as in *Apseudes*, there is given off from every pair of ganglia two pairs of nerves, of which one pair (M.N) supplies the muscles in the segment in which the ganglia lie, and the other (S.N) some sensory surface, like the skin; hence the former are called **motor** and the latter **sensory nerves.**

In *Astacus* the viscera is enervated by a sympathetic nervous system formed as follows: on each circum-œsophageal commissure, just by the side of the œsophagus, is a small ganglion from which a nerve runs upwards, each joining on the top of the stomach, where they receive a small nerve from the cerebral ganglion. From the union of these a **visceral nerve** (V.N) is formed which runs back over the alimentary canal.

Cockroach. In its general features the nervous system of the cockroach is similar to that of the crayfish. It consists of a large bilobed mass lying in the head, the **cerebral ganglion**, from which paired **optic** and **antennal nerves**, the latter with swollen roots, pass off. The brain is connected with the infra-œsophageal ganglion by an œsophageal commissure; the nerves passing from the ganglion supply the mandibles and the first and second maxillæ. In the larva of many insects, this ganglion is represented by three pairs, which fuse before the imago stage is completed; hence we infer that the oral region is composed of three fused segments.

The two parts of the infra-œsophageal ganglion each give off from behind a ventral cord which runs the whole length of the trunk, and

bear ganglionic enlargements for each segment of the body, except in the last four abdominal. The first three pairs of these ganglia are larger than the rest and lie in the thorax, the muscles and appendages of which they supply. In the abdomen there are six smaller pairs of ganglia which lie in the first six segments; the last of these is larger than the others, and further differs from them in supplying the four segments behind, as well as the one in which it lies. The full number of ganglia is never found in any insect imago or larva, but in some embryos ten ganglia are present, the hinder ones of which, as development proceeds, fuse together from behind forwards. We must, therefore, regard the last abdominal pair of ganglia in the cockroach as resulting from the confluence of four pairs. The longitudinal commissures are paired and separate along the whole length of the nerve cord. The sympathetic nervous system is composed of a paired and an unpaired portion. It arises as a pair of nerves from the œsophageal commissure, each of which gives off at once a nerve to the upper lip, and then unite in front of the œsophagus to form the **frontal ganglion.** From this there passes back a median **recurrent nerve,** which a little behind and under the cerebral ganglion joins two pairs of ganglia, the **anterior** and **posterior visceral ganglia,** which are connected with the brain; from these ganglia nerves are given off to the salivary glands and the œsophagus. The recurrent nerve, passing backwards over the crop, reaches a small, triangular ganglion from which two nerves run obliquely backwards.

Fresh-water Mussel. The nervous system of this animal consists of three pairs of ganglia connected by paired commissures.

The **cerebro-pleural ganglia** (Fig. 74, C-P.G) lie just behind the anterior adductor muscle, and just in front and on either side of the short œsophagus; they are connected together by a short transverse commissure. The **viscero-parietal** or **parieto-splanchnic ganglia** (V-P.G) lie on the ventral surface of the posterior adductor muscle; each ganglion is constricted in the middle, and looks as though it were composed of two confluent ganglia. They are connected with each other by partial confluence in the middle line, and with the cerebro-pleural ganglia by a paired commissure (COM) which passes through the whole length of the organ of Bojanus (U) and the substance of the liver (L). The **pedal ganglia** (P.G) lie in the foot, at its junction with the body, and are closely apposed; they are connected to the cerebro-pleural ganglia by the **cerebro-pedal com-**

missures (COM). The cerebro-pleural ganglia innervate the labial palps, the anterior adductor muscle, mantle, and adjacent parts; the viscero-parietal, the posterior adductor muscle, mantle, ctenidia, osphradia, and the viscera; and the pedal, the muscles of the foot and the otocyst or supposed auditory organ.

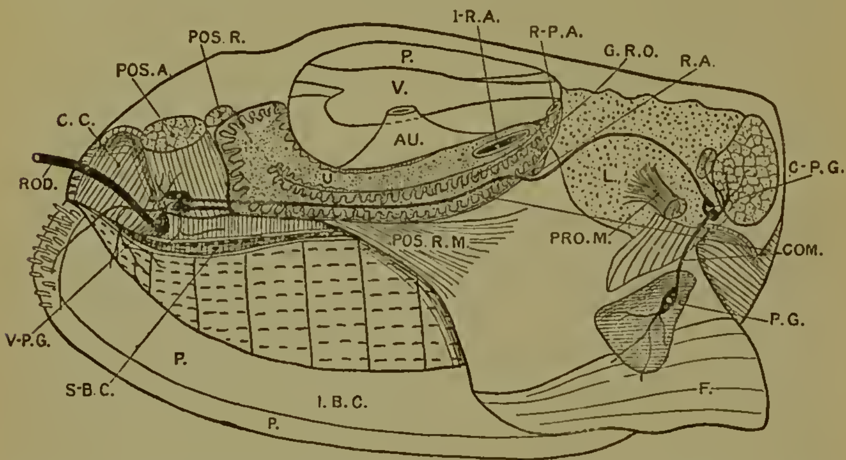


FIG. 74. Side dissection to show nervous, renal, and circulatory systems of *Anodonta* (Fresh-water Mussel). AU = auricle of heart; C-P.G = cerebro-pleural ganglion; COM = commissures; C.C = cloacal chamber; F = foot; G.R.O = glandular part of renal organ (organ of Bojanus); I.B.C = infra-branchial chamber; I-R.A = inter-renal aperture; L = liver; P (upper one) = pericardium; P (lower one) = pallium or mantle; P.G = pedal ganglion; POS.A = posterior adductor; POS.R = posterior retractor; PRO.M = protractor muscle of foot; POS.R.M = insertion of posterior retractor muscle in body; R-P.A = reno-pericardial aperture; R.A = renal aperture; ROD = rod inserted in supra-branchial chamber (S-B.C) of left side; U = ureter of renal organ; V = ventricle; V-P.G = viscero-parietal ganglion.

When we compare the nervous system of *Anodonta* with that of a more primitive lamellibranch, such as *Nucula*, we find that in the latter there lies upon the commissure that connects the cerebral and viscero-parietal ganglia, a little behind the former, a small pleural ganglion, the commissure of which, after remaining free for the greater portion of its length, unites with the cerebro-pedal commissure near the pedal ganglia. Here we have evidence of the existence in the oral region of two distinct pairs of ganglia; and since the single pair of ganglia in *Anodonta* innervate the same region as that supplied by the two pairs of ganglia in *Nucula*, there is reason to believe that the cerebro-pleural ganglia of the former have resulted from the fusion of the pleural and cerebral ganglia of the latter. Such a conclusion is further rendered probable by the condition which is exhibited in *Solenomya*, where, although the pleural and cerebral ganglia are still

distinct, the pleuro-pedal commissure is fused along its length with the cerebro-pedal commissure; compared with that in *Nucula*, we have here evidence of the fusion of these parts actually taking place, the final stage of which is reached in *Anodonta*. *Nucula*, *Solenomya*, and *Anodonta* thus represent, in virtue of the condition of the pleural and cerebral ganglia, three stages in the process of confluence or concentration of a certain part of the nervous system.

Interesting though the comparison of these three lamellibranchs may be, more interesting still is the comparison of these with the Gastropoda or snails. In them there is a pair of cerebral ganglia lying in front of the alimentary canal and connected by two pairs of commissures with the paired pedal and pleural ganglia, which lie behind and ventrad of the œsophagus. The pleural ganglia are connected with the pedal by a paired commissure, and also by another pair of commissures with two other ganglia, lying posteriorly to them, i.e. an unpaired visceral and parietal ganglion, lying more or less in apposition to one another. In some gastropods there are two parietal and two or more visceral ganglia.

Now assuming that the pedal ganglia of the Gastropoda were to be displaced in a ventral direction, with a corresponding lengthening out of the cerebro-pedal commissures, and that the parietal and visceral ganglia became fused, we should have the condition presented by such a lamellibranch as *Nucula*. Assume further that the pleuro-pedal commissures fused with the cerebro-pedal, and we should repeat the condition of *Solenomya*; while, if the pleural and cerebral ganglia themselves fused, there would be produced the condition of *Anodonta*. Thus we can interpret the nervous system of *Anodonta* in terms of that of the snails, by assuming that the fusion of certain parts and the displacement of others has taken place. That this assumption is not a false one, is rendered clear by the condition of the nervous system in certain primitive lamellibranchs and in certain Gastropoda; among the latter, *Bulla* shows an approximation of the pleural and cerebral ganglia, while in *Actæon* they have actually fused.

If the viscero-parietal ganglia of *Anodonta* have been derived by the fusion of the paired parietal and visceral ganglia of the Gastropoda, then we should expect that the area innervated by the former should be the same as that by the two latter. In the Gastropoda the visceral ganglion supplies the viscera, and the parietal, the ctenidia, osphradium and mantle. The fused viscero-parietal ganglion of the lamellibranchs supplies the same regions. The evidence therefore seems quite clear,

and justifies the conclusion, that the cerebro-pleural ganglion of *Anodonta* corresponds to the cerebral and pleural ganglia of the snails; that its viscero-parietal corresponds to the separate visceral and parietal ganglia of them; while the pedal ganglia are the same in both.

Earthworm. The nervous system of *Lumbricus* consists of a distinctly bilobed **cerebral ganglion** (Fig. 75, C.G) lying in the third segment on the dorsal surface of the buccal sac (B.S), at the junction of that with the pharynx. There proceeds backwards from it a paired circum-œsophageal commissure (C.C), which meets beneath the pharynx, in the infra-œsophageal ganglion, lying just behind the third segment. Behind the infra-œsophageal ganglion there is a paired nerve cord, lying on the ventral body-wall, in the mid-line: the two nerve cords are closely apposed and are bound together in a common sheath (Fig. 76, N.C). The nerve cord is metamerically enlarged, but the enlargements are not so markedly ganglionic as those in the crayfish, since they are much longer in proportion to their width; from each enlargement three pairs of nerves are given off, of which only two are represented in the figure.

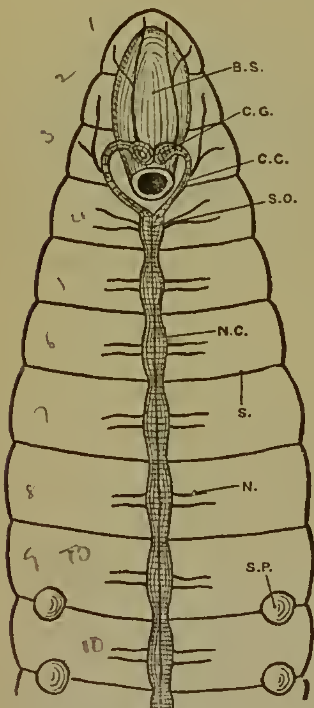


FIG. 75. Dorsal dissection to show nerve cord of Earthworm (*Lumbricus*). The alimentary canal has been removed as far forward as the buccal sac. C.C = circum-œsophageal commissure; C.G = cerebral ganglion; B.S = buccal sac; N = nerves; N.C = nerve chain; S = septa; S.O = sub-œsophageal ganglion; S.P = spermothecæ.

Examined by means of transverse sections (Fig. 76, N.C) beneath the microscope, the nerve cord is seen to be very apparently double, the two nerve trunks being in contact in the middle line, and surrounded by a common sheath of fibrous tissue. Along the dorsal surface of the cord and embedded in the sheath are three tubular fibres, of which the middle one is larger than the others; they are known by the name of **giant nerve tubes** or **neurochord strands**, and probably represent the metamorphosed neurilemma sheaths of giant nerve fibres which arise from giant ganglion cells

situated at different parts of the nerve cord. There is reason to believe that the nerve fibres degenerate, leaving the neurilemma with a central canal, which becomes filled with a watery fluid. The function of the giant nerve tubes is probably that of supporting and strengthening the nerve cord.

The nervous portion of the cord is composed of a granular looking substance, the granules representing the cut ends of nerve fibres; embedded in the ventral portion of this, and to some extent in the lateral portions, are large pear-shaped, unipolar ganglion cells, with a large nucleus and nucleoli.

The lateral and sub-neural blood-vessels will be seen cut across, lying in the substance of the sheath.

CHAPTER XIV

EXCRETORY OR RENAL ORGANS

Excretion is the extraction from the blood-stream of certain material which has resulted from the living activities of the tissues. The object of the excretory organs, after having extracted the material from the blood, is to eliminate it from the body by the quickest path.

The characteristic feature of the excretory organs of cœlomate Invertebrata, when they are well developed, is that they are tubular organs opening on the one hand into the cœlom or body cavity, and on the other to the exterior. So constant is this relationship that, when we find an excretory organ opening from a cavity which may be small and restricted, and may not at first sight look like a body cavity, we regard it as having a good provisional claim to be such, because of its connexion through the organ of excretion with the exterior.

Organs of excretion, which maintain a more or less obvious tubular character, are called **nephridia**, and their funnel-like, terminal expansions at their cœlomic extremity **nephrostomes**.

Excretory organs may be experimentally demonstrated to be such by feeding the animal under investigation with some pigment, such as carmine, indigo-carmine, and Bismarck brown, finely divided and suspended in the water in which the animal is living. After having thus been fed for a longer or shorter period, the animal is killed, and the tissues either examined fresh or after suitable preparation. Those

tissues which are excretory in nature will be found to be laden with the pigment and to be in the act of eliminating it from the system, while those which are not excretory will contain no pigment.

Crayfish. In many respects the excretory organ of the crayfish is interesting, if for no other reason than that its real morphological nature is not certainly determined; it has been stated to arise as a dermal depression, when it would be of ectodermal origin, whereas observations on other Crustacea show that in them the excretory organ is of mesodermal origin.

Throughout the Crustacea there are to be found two excretory organs, one related to the antenna and called the **antennal gland**, and the other situated in a fold of the shell in a region which corresponds to the second maxilla, called the **shell gland**. In some Crustacea these two glands are to be found together through all periods of life; in others, one gland may be found in the larva and the other in the adult, the first gland disappearing before adolescence is reached; while in others, only one of the two glands is present at any period of life. From their wide distribution in most of the Crustacea, we may infer that they are very ancient organs, and are probably derived from the racial forms of the Crustacea, from which the living forms are descended. The two glands are similar in structure, and this fact, when taken in conjunction with their constant position—the antennal gland in the base of the posterior antenna, and the shell gland in the segment of the second maxilla—would seem to indicate that they are serially homologous organs.

In the crayfish only one of these glands is present, i. e. the antennal gland, and it is called the **green gland**, on account of the pale green colour of its glandular portion. It lies in the head portion of the cephalo-thorax (Fig. 69, G.G), and when examined by the ordinary methods of dissection is seen to consist of two portions, a ventral, pale green, glandular (G.G), and of a dorsal, membranous sac, the **ureter** (U), which opens to the exterior (R.A) upon the basal joint of the antenna (AN). When examined by microscopical methods, the glandular portion can be resolved into a single tube, intricately coiled upon itself, and composed of cells arranged one behind the other like a pile of coins, and which are pierced by a canal, the **urinary canal**, which runs the whole length of the tube. The urinary canal is thus **intra-cellular** in nature, i. e. it pierces the substance of the cells; this condition is one in contrast to that where the lumen or channel of a tube is formed by the arrangement of cells round it, so that the lumen runs

between a circular layer of cells, and is **inter-cellular** in nature. At either extremity the glandular tube is terminated by sac-like expansions, which are, however, different in nature. That which is situated at the distal end of the tube is merely an expansion of that, and is lined by the same epithelium; it constitutes the ureter mentioned above. The other, the **terminal sac**, is much smaller and is lined by a flattened epithelium, quite different to that lining the renal bladder.

The coiled urinary tube opens, therefore, on the one hand to the exterior and on the other to the cavity of this terminal sac, which the facts of development show is a portion of the cœlom. With the exception of this small cavity and that in the gonads (ovary and testis), the cœlom is otherwise unrepresented in the crayfish.

Cockroach. The excretory organs (Malpighian tubules) have already been described (ante, p. 250).

Mussel. Like that of the crayfish, the renal organ of *Anodonta* is symmetrical and paired. It is called the **organ of Bojanus**, and lies (Fig. 74, G.R.O & U) immediately beneath the pericardium (upper P) and behind the posterior adductor muscle (POS.A), and can be easily seen on account of its black colour. Essentially it is a tube doubled once upon itself, one end of which opens into the anterior end of the pericardium (R-P.A), and the other by a small aperture, whose lips are slightly thickened (R.A), into the supra-branchial chamber of the inner gill, which in its turn communicates with the exterior through the cloacal chamber (C.C). The ventral limb (G.R.O) of the loop has a spongy wall, formed by lamellar foldings, and the epithelium which lines its cavity is deeply pigmented. The dorsal limb (U) is a simple tube, and serves to carry the excretory products to the exterior; it is termed the **ureter**.

The two organs of Bojanus lie in apposition in the middle line, and the ureters (dorsal limbs) are in communication with each other through a large slit-like aperture, the **inter-renal aperture** (I-R.A).

Lumbricus. The excretory organs of the earthworm consist of segmentally arranged tubes (Fig. 71, N), one pair to each segment of the body. Each tube is folded into three U-shaped loops, in two of which the tube is narrow and small, and the third much larger (Fig. 76, N). Each nephridium opens into the cœlom by a ciliated, wide-mouthed funnel, the aperture of which is called the **nephrostome**; the funnel leads into a very slender tube, which runs backwards and pierces the septum (Fig. 71, S) that divides the cœlom of this segment from that next behind it, when it runs an irregular course along both

limbs of the short loop and part of the long loop. It then turns upwards and runs nearly to the dorsal surface of the alimentary canal, then turns back again towards the ventral surface (Fig. 76), thus forming the long first loop, at the bend of which the tube is somewhat

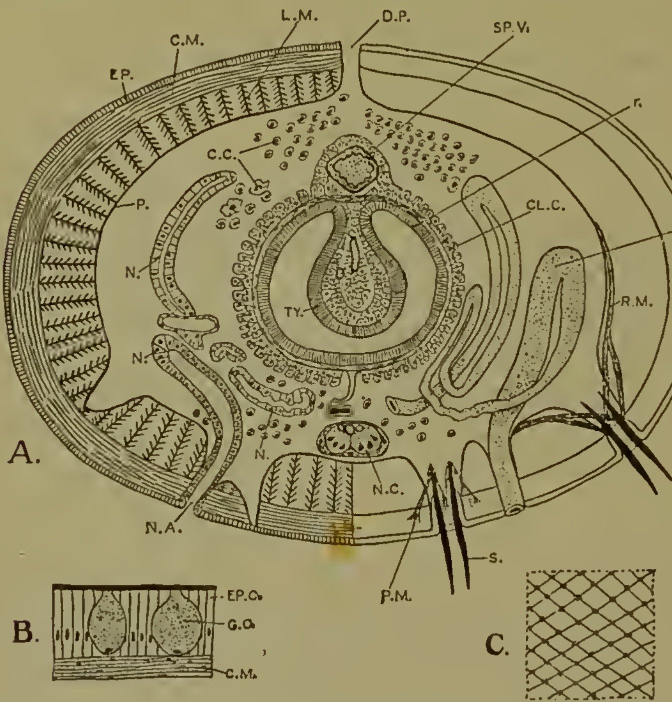


FIG. 76. A. Transverse section through the intestinal region of the Earthworm (*Lumbricus*). On the left hand all the parts are represented as they actually are seen in a section. On the right the nephridium is reconstructed from a series of sections and is slightly diagrammatic, and only one set of muscles is represented for each pair of setæ; the true relation would be represented if the two sets of muscles (R.M and P.M) were represented for each pair. B. Portion of the ectoderm (epidermis) and circular muscle layer under the one-eighth objective. C. Surface view of a piece of cuticle, stripped off and examined in salt solution under the one-eighth objective. C.M = circular muscular layer; CL.C = chloragogen cells; C.C = cœlomic corpuscles; D.P = dorsal pore; E.P. = epidermis; EP.C = epidermal cells; G.C = goblet cells (unicellular glands); I = intestine; L.M = longitudinal muscle layer; N = nephridium (on the left the different parts are seen in section, and on the right as they would appear as solid objects); N.A = nephridial aperture; N.C = nerve cord; P = peritoneum; P.M = protractor muscle; R.M = retractor muscle; S = setæ; SP.V = supra-intestinal blood-vessel; TY = typhlosolis.

dilated to form the ampulla. The tube then turns slightly inwards and forms another loop, only about one-third the length of the first. The descending limb of this then turns outwards and upwards, and passes somewhat suddenly into the much thicker terminal loop, which opens to the exterior, between the lateral and ventral setæ (Fig. 76, S).

The first or narrow portion of the tube is ciliated along part of its course, but not the whole, and its duct or lumen is intra-cellular. The second part of the tube is formed by the proximal or ascending limb of the first or long loop, and its duct is ciliated and intra-cellular. The third part of the nephridium is formed by the descending limb of the first loop, the two limbs of the short loop, and the first part of the proximal limb of the third loop; the duct is wide, non-ciliated, and intra-cellular. The last part of the tube or bladder is formed by the greater portion of the proximal and the whole of the distal limb of the third loop; its lumen is very wide, non-ciliated, and inter-cellular.

Each nephridium is supplied by a blood-vessel from the supra-neural vessel (Pl. II, Fig. 3), which breaks up into capillaries over the wall of the long and short loops, and from which the blood is carried by another small vessel to the sub-neural vessel.

The nephridia of the earthworm open to the exterior upon the segment next behind that in which they communicate with the cœlom (Fig. 71).

CHAPTER XV

THE REPRODUCTIVE SYSTEM

Crayfish. In the more primitive Crustacea the gonads or germinal glands are paired. In the crayfish they still retain their primitive paired nature in the anterior region of the gland and in the independence of the two ducts along their whole length.

The sexes are distinct in the crayfish, as in all Crustacea, the parasitic ones excepted. The gonads in both sexes are situated between the heart and the intestine (Fig. 69, T & T′), and extend slightly in front and behind the heart. The sexual organ consists of two portions: a gland which produces the sexual material and called the **gonad**—**ovary** in the case of the female and **testis** in that of the male—and of paired **sexual ducts**, the **vas deferens** and **oviducts** in the male and female respectively, which serve to convey the sperm and ova to the exterior.

The ovary (Fig. 77) when ripe has a tuberculated surface with a yellow colour, due to the presence of yellow yolk-granules (nutritive particles) in the ripe eggs. In form it is somewhat trilobed, of which

two lobes are directed anteriorly (Fig. 77, ANT.R.L) and the third (POS.M.L), lying in the middle line, beneath the heart, posteriorly. When opened it is seen to contain a cavity, into which a number of globular sac-like processes project from its wall; these are the **ovisacs**, each of which contains an **ovum** or **egg-cell**, surrounded by a single layer of much smaller cells, which are separated from the cavity of the ovary by the structureless membrane which forms its general lining. Each ovum when mature is limited externally by a thin, structureless, **vitelline membrane**, enclosing a very granular protoplasm of deep brownish-yellow colour, and containing embedded in its mass a **germinal vesicle** with **germinal spots**. The germinal vesicle represents a metamorphosed nucleus, and the germinal spots the nucleoli. When the ovum is quite ripe, the ovisac bursts and liberates it into the cavity of the ovary, whence it passes through the oviducts (Fig. 77, OD) to the exterior. The latter are two short, wide tubes arising from either side of the ovary at the junction of the paired with the unpaired portion, and which pass backwards and downwards, to open to the exterior upon the coxopodites of the third ambulatory appendages.

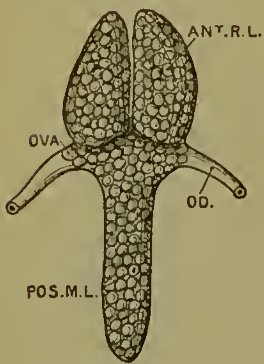


FIG. 77. Dorsal view of the ovaries of the Crayfish (*Astacus*). ANT.R.L = anterior right lobe; POS.M L = posterior median lobe; OD = oviduct; OVA = ova passing into oviduct.

The **testes** in general form are like the ovaries, but differ in the greater length of the median, unpaired lobe. When mature they are opaque white in colour, but translucent while unripe. Their cavity is more or less filled by an immense number of minute spheroidal vesicles attached to the ends of short stalks, which are of the same morphological nature as the ovisacs of the ovaries. The cavity of each vesicle is filled by the large nucleated cells which line its walls, and which multiply by division as the breeding season approaches. Each of these cells will give rise to a **spermatozoön**, which is the male equivalent of the female egg. But they first pass through a remarkable series of changes, the final result of which is the production of a star-like body, with very long, slightly curved rays attached to a central flattened discoidal centre. The latter is composed of a granular protoplasm, lodging in its middle a vesicle with a granular body within it, the whole being called the **annulate corpuscle**; and

peripherally to this there is a zone of protoplasm with an excentrically situated nucleus, and known as the **spheroidal corpuscle.**

The **vas deferens** or male sexual ducts arise from the junction of the paired with the unpaired portions of the testes (Fig. 69, V.D). These are at first very thin, and before passing into the thicker and coiled portion describe a number of coils which ultimately open to the exterior upon the coxopodites of the fifth ambulatory, or last thoracic appendage. They are opaque white in colour, due not only to the presence of the spermatozoa, but also to a viscid material secreted by the walls of the vasa deferentia, and which serves to bind the spermatozoa together when they are deposited upon the last thoracic and first abdominal sterna of the female. Here it forms a chalky-looking mass, whence probably the spermatozoa fertilize the eggs as they pass out from the apertures of the oviducts. Exactly how the spermatozoa reach the eggs is not known, but analogy of what occurs in other animals leaves no doubt that actual mixture of the male and female elements takes place.

The eggs when they leave the oviducts are transferred to the swimmerets of the female crayfish, to which they become attached by means of a viscid material which surrounds them and that hardens upon exposure. Here the fertilized eggs undergo the early stages of development, up to the period when the young can swim about for themselves. They are, however, often carried about under the cover of the mother's telson for some time after their liberation from the egg.

Cockroach. The sexual apparatus of the cockroach, though referable to the same fundamental plan as that of the crayfish, is rendered much more complex on account of the presence of accessory portions.

The **ovaries** consist of two sets of eight tubes, which unite behind to form two oviducts that open separately into a short tubular canal, the **vagina**, formed by invagination of the integument; the vagina opens to the exterior upon the eighth abdominal sternum. Each **ovarian tube** is moniliform or beaded in outline, due to the presence of the contained eggs; the youngest egg is at the apex of the tube, and the oldest or most mature at the base—the end at which the tube opens into the oviduct.

As already described in the chapter dealing with the exoskeleton of the female, the sterna of the hinder segments, i.e. eighth to tenth, are invaginated, and the seventh is prolonged backwards, thus forming a pouch-like chamber, into which the sexual apertures open. From the sternal surfaces of the eighth and ninth segments certain cuticular

processes project, called the **gonapophyses** ; they are instrumental in arranging the eggs within the capsule as they pass into the gonapophysial chamber from the oviducts. The egg capsule is formed by the secretion of the **colleterial glands** ; and the eggs are laid, one from each ovarian tube, thus making sixteen in all, in the gonapophysial chamber, where they become enclosed in the colleterial secretion which, upon hardening, forms an investing capsule.

The **spermothecæ** or **receptacula seminis** open into the gonapophysial chamber upon the ninth sternum, in front and above the aperture of the vagina. They consist of a pair of cæca, one of which is more or less club-shaped, while the other is merely tubular, following a somewhat convoluted course. They receive the sperm from the male during the act of copulation.

The **colleterial** or **cement glands** are a pair of much branched tubular organs which open, each by a single aperture, upon the tenth abdominal sternum, and between two of the gonapophyses.

In the male the **testes** are paired ; they each consist of a large number of very short, small tubes, which are grouped together in a mass ; all the testical tubules of either side open into a single **vas deferens**, which in its turn opens into a **vesicula seminalis**, a somewhat dilated sac that gives origin to a large number of blind tubular cæca, arranged in two groups, and called the **mushroom-shaped gland.** From the vesicula seminalis there proceeds a short, muscular tube, the **ductus ejaculatorius**, which opens to the exterior upon the last segment, just behind the anus. In the male, as in the female, there are a series of gonapophyses, which in the former form a complex copulatory organ, by means of which the sperm is guided into the receptaculum seminis of the latter.

Fresh-water Mussel. In the mussel the sexes are, as a rule, distinct ; though occasionally, eggs and spermatozoa are developed in the same gonad, which do not however ripen simultaneously.

The gonad (Fig. 72), **ovary** or **testis** as the case may be, lies among the folds of the intestine, and its contents fill the body cavity between the intestinal and body-walls above the muscular foot. They are paired and symmetrical, the two glands lying in apposition in the middle line. They each open directly to the supra-branchial chamber of the inner gill of either side by a single short germinal duct—**oviduct** in the female and **vas deferens** in the male.

In the male the spermatozoa, when discharged, are swept out from the supra-branchial chamber by the respiratory stream of water into

the water in which the animal is living, whence it is carried, through the inhalent apertures of female mussels, to fertilize the ova.

The ova, after they leave the genital duct, pass into the space between the two lamellæ of the gills, this space being continuous above with, and indeed is part of, the supra-branchial chambers. Each ovum is a spherical mass of granular protoplasm, with a germinal vesicle and spots; at one part its substance is prolonged into a blunt-like process, which projects slightly through an opening, the micropyle, in the structureless vitelline membrane which surrounds the egg. This latter does not closely invest the egg as in the majority of cases, but only loosely, the interval between the membrane and the egg being filled with an albuminous fluid.

The eggs are fertilized and undergo their development into embryo mussels while still within the cavity between the gill lamellæ. The organisms which thus arise are in many respects different from the adult, and are called **glochidia**. Each glochidium larva consists of two shells, closed by a *single* adductor muscle; the shell covers a very rudimentary body, in which only traces of the mid-gut exist, the communication of this with the fore- and hind-guts not yet having taken place. The foot is represented by a small swelling, and the real mantle and gills are absent. On the ventral body-wall there is a gland which secretes a long thread-like process, called the **byssus**, that serves as an adhesive organ, by means of which the larva becomes attached to some portion of the integument of a fish. The shell of the larva is triangular in form, and the ventral apex is armed by a number of tooth-like spines, by which the organism pierces the skin of the fish to which it has become attached by its byssus. The wound thus inflicted causes the skin to swell to such a degree that the glochidium larva becomes encompassed in it. Protected and nourished in this manner, it passes through its metamorphosis and becomes a mussel, differing at first from the adult in the absence of the genital organs and the outer gills. At this stage in its development, it is liberated by the bursting of the capsule in the skin of the fish and falls to the bottom of the water, where it passes the remainder of its existence.

The adoption of this parasitic mode of life during its larval development is of a twofold advantage to the organism; for, firstly, it prevents the very young larva from being washed away and destroyed by streams, while its period of existence in the skin of the fish is partly protective, partly nutritive; and secondly, the situation at which the young mussel will be dropped when the integumentary capsule of

the fish bursts may be many miles from that where it was liberated from the parent. Its mode of larval life, therefore, is not only adapted to ensure the maintenance of the species in time, but also, to a certain extent, to widen its geographical distribution. The latter is but a means towards the attainment of the former, for organisms crowded together into a small, localized area soon exhaust the food supply.

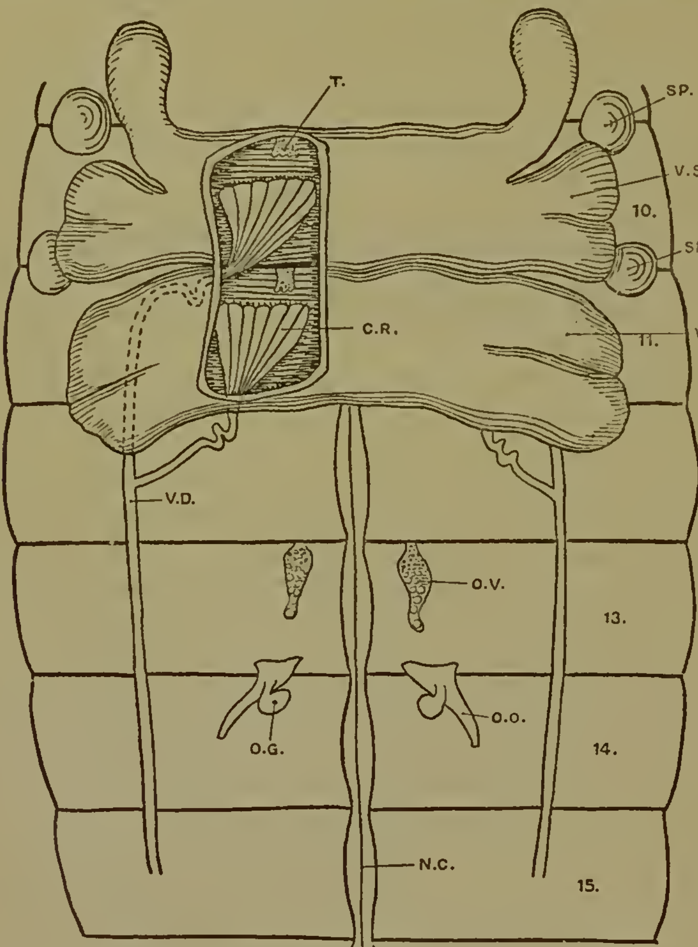


FIG. 78. Dorsal dissection to show genital organs of Earthworm (*Lumbricus*). The body-wall has been cut open along the mid-dorsal line and the alimentary canal removed. C.R = ciliated rosette (funnel of vas deferens); N.C = nerve cord; O.D = oviduct; O.G = receptaculum ovorum (oviducal gland); O.V = ovary; SP = spermothecæ; T = testis; V.D = vas deferens; V.S = vesiculæ seminalis. The numbers refer to that of the body segment in which they are placed.

Earthworm. In the earthworm the genital organs are confined to the ninth to fifteenth segments.

The **testes** (Fig. 78, T), or male gonads, consist of two pairs of very small bodies, lying in segments ten and eleven, and attached on either side of the middle line to the posterior faces of the septa belonging to those segments. The posterior lamellæ of these two septa give rise to two median sac-like organs, the **sperm capsules** or median **vesiculæ seminales**, which enclose the testes, one pair in each capsule. The anterior sperm capsule gives origin to one and the posterior to two pairs of lateral outgrowths, the **sperm sacs** or **lateral vesiculæ seminales** (V.S). The number, however, is not constant, and frequently more may be developed. Situated in each sperm capsule, immediately behind the testes, are a pair of funnels, called the **ciliated rosettes** (C.R), because their walls are much plicated in a rosette fashion and are ciliated. Each of these funnels leads into a tube, the **vas deferens** (V.D); the two on the same side of the body unite to form a single tube, which runs, partially embedded in the body-wall, to the middle of the fifteenth segment, where it opens to the exterior.

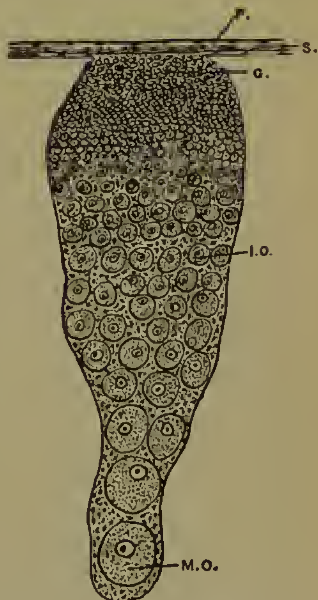


FIG. 79. An ovary and part of a septum of the Earthworm (*Lumbricus*). Fixed in spirit, stained with eosin and clarified in oil of cloves, and examined under the one-sixth objective. G = germinal mass of undifferentiated cells; I.O = the germinal cells differentiating into ova; M.O = a mature ovum; P = peritoneum; S = septum.

The testes never attain to a great size, for at a very early period they break up into the formative cells of the spermatozoa; these former are liberated from the testes into the sperm capsule and sacs, and here undergo the early changes that finally result in the production of ripe spermatozoa, the nature of which will be best understood when the remaining sexual organs have been considered.

The **spermothecæ** (Fig. 78, SP) or **receptacula seminis** are two pairs of globular sacs, situated and opening to the exterior between segments nine and ten and ten and eleven.

The **ovaries** (O.V) are two pairs of conical bodies, attached by their base to the posterior face of the anterior septum of segment thirteen. Each ovary (Fig. 79) is covered by a layer of peritoneal epithelium (P), within which, at the basal end, are a large number of undifferentiated cells (G), from which the ova arise. At the

apex of the ovary there is one large spherical cell (M.O), with granular protoplasm, a prominent germinal vesicle, and germinal spots; this is a ripe ovum, and will be thrown off into the cœlom by the constriction of that portion of the ovary just behind it. Behind the mature ovum there are one or two large cells, arranged in single file, and having the same appearance as the ripe ovum; these are ova which are nearly ripe. Between these and the basal portion of the ovary there are a group of other cells, which from their character are obviously ova, but as yet are far from ripe; these pass imperceptibly into the undifferentiated mass mentioned above.

The **oviducts** (Fig. 78, O.D) are a pair of short tubes, opening into the cœlomic space of the thirteenth segment by a funnel-like aperture; they pass backwards and slightly outwards and pierce the body-wall in about the middle of the fourteenth segment, when they open to the exterior. Opening into the funnel-like mouth of each oviduct is a reniform sac, the **receptaculum ovorum** (O.G), which is distinguishable in an ordinary dissection by its red colour, due to its rich vascular supply.

The earthworm is thus seen to be hermaphrodite, in the sense that every individual possesses both male and female organs; but it is not self-fertilizing, since the sperm derived from the testis of one individual does not fertilize the ova of the same.

The processes which precede and lead to the final act of fertilization are somewhat complex, and require the co-operation of two worms. If we pay a visit to a lawn or plot of ground in which worms are known to be, after ten o'clock at night, we may find that two of them are partially protruded from their burrows and are applied together by their ventral surfaces in such a way that the fifteenth segment (that upon which the vas deferens opens to the exterior) of one worm is opposite one of the pair of apertures of the spermothecæ of the other. The first worm is in the act of passing unripe sperm from its sperm-sacs through its vas deferens into the spermothecæ of the second, where the sperm will complete the process of ripening.

If we examine any worm which is sexually mature, we shall find that from about the thirty-second to the thirty-seventh segment the dorsal and lateral surfaces of the integument is much swollen; microscopic examination of this region shows that this swelling is due to the presence of glandular cells in the epidermis, and that they are engaged in the formation of a chitinous investment of this region of the body. When the sperm introduced into the spermothecæ and the ova are quite ripe, the worm begins to wriggle backwards out

of this chitinous ring, and, in so doing, brings first the apertures of the oviduct on the fourteenth segment and subsequently those of the spermothecæ between segments nine and ten and ten and eleven into it. As these apertures pass into the chitinous ring they each discharge their contents, i.e. the oviducts the eggs, and the spermothecæ the ripe sperm. Ultimately the head segment of the worm passes through the ring, when the two apertures close, and the ring thus forms a capsule containing the eggs and spermatozoa. The capsule soon hardens and forms a **cocoon**, within which the fertilization of the eggs take place and the early stages of development proceeds.

The **formative cells** or **spermospores**, when liberated from the testis, each consists of a single cell with a well-defined nucleus. Each cell divides into two, and these two into four. In the process of division, however, some portion of the protoplasm of each of the four cells aggregates towards the centre and becomes slightly more granular. This, which may be called the passive portion of the protoplasm, increases in quantity as the process of division goes on, so that, at a certain stage, there is formed a spherical mass of passive protoplasm, with rounded, shortly-stalked cells attached to its surface. Viewed from the surface this mass presents a somewhat mulberry-like appearance; it is called a **spermospore**, and each stalked cell a **spermoblast**. As maturation proceeds each spermoblast lengthens considerably, its nucleus increasing in size out of all proportion to that of the cell itself. When nearly ripe, a spermoblast consists of an elongated nucleus attached by one extremity to the central passive protoplasm, and bearing at the other a small vesicle from which a long filament proceeds; the vesicle and filament represents the protoplasm of the cell, which is much reduced when compared to the size of the nucleus. At about this stage in development, or slightly earlier, the spermospores are transmitted, in the manner already described, to the spermothecæ, where they complete the process of maturation. While here the spermoblasts lose the small vesicle and become separated from the central mass of passive protoplasm: they are now called **spermatozoa**, and each consists of a **head**, derived from the nucleus, and a vibratile **tail** derived from the protoplasm of the spermoblast.

We thus see that of the original formative cell the nucleus is the important, and also, as we shall later learn, the essential part. It gives rise by repeated divisions to a large number of spermatozoa;

the protoplasm of the cell, for the most part, becoming aggregated to form a central passive mass, a small portion only taking part in the formation of the tails of the spermatozoa.

The passive portion of the protoplasm probably at first serves as a nutritive material, by the absorption of which the nuclei are enabled to grow, and subsequently it gives rise to a fluid-like material in which the spermatozoa swim about. It is this fluid which is injected into the cocoon as the worm wriggles backwards and in which the ova become immersed ; the spermatozoa contained within it thus come into contact with the eggs. Each egg is then penetrated by a spermatozoön, the nucleus of which fuses with that of the ovum ; this is the final act, and is called the **fertilization of the egg.** The outcome of fertilization is the production of an embryo, by processes which we shall study when dealing with the phenomena of fertilization and development.

CHAPTER XVI

COMPARISON OF THE GENITAL DUCTS WITH THE NEPHRIDIA

In the course of the two preceding chapters we have seen that in the earthworm there is a series of segmental tubules having a renal function, which open on the one extremity to the cœlom, and on the other to the exterior. So that, had we no further facts to go upon, we should regard a nephridium as being a tubular organ placing the cœlom in direct communication with the exterior. And, if such be the true definition of a nephridium, it is obvious that we must regard the genital ducts and the green gland of the crayfish, the organ of Bojanus of the mussel, and the genital ducts of *Lumbricus* as modified nephridia ; for all these organs conform to such a definition. In the crayfish, the cavity of the terminal sac of the green gland, and the cavity of the gonad, are known to be from their development remnants of the cœlom ; in the mussel, the pericardium, with which the organ of Bojanus communicates at its inner end, is likewise a cœlomic cavity; and the cavity of the vesiculæ seminales in the earthworm, with which the vas deferens communicate by their ciliated rosettes, is a portion of the cœlom cut off from the general body-cavity, and the oviducts open directly in the cœlomic cavity of the segment in which they lie.

Based upon considerations of this kind, zoologists formerly con-

founded two distinct organs, i. e. the genital ducts and the true nephridia, and regarded the genital ducts in some cases (as in the crayfish) as representing modified nephridia. And this conclusion seemed to be corroborated by the fact that in some worms certain of the nephridia became modified at the breeding season to function as genital ducts.

In 1895 Goodrich called attention to the fact that the cœlom was really a derivative of the gonadial cavity, which arises in the mesoblast, and that the genital ducts arise as tubular outgrowths of this. He further showed, as the result of a compilation of a large number of independent researches, that true nephridia arise from the epiblast and grow *inwards* towards the cœlom, and that their tubular cavities are intra-cellular; whereas genital ducts grow *outwards* from the cœlom as tubular evaginations of that, and their cavities are inter-cellular. Obviously these embryological data afford a crucial test enabling us to determine whether a given duct is nephridial or genital.

Appealing to such facts we find that the green gland of the crayfish and the shell gland of other Crustacea are not true nephridia, but that they must be regarded as modified genital ducts which have assumed a renal function ; for the green gland arises as a tubular *outgrowth* from the cœlom, and is therefore mesoblastic in origin. It is, therefore, homologous, not to the nephridia of the earthworm, but to the genital ducts of that animal and of itself [1].

The same conclusion holds for the organ of Bojanus in the mussel ; it is not a true nephridium, for it does not arise from the epiblast, and its cavity is not intra-cellular. It arises like a true genital duct as an *outgrowth* of the gonadial (cœlomic) cavity, and is thus mesoblastic in origin. The cœlomic cavity in the course of development becomes constricted into two portions, one part of which becomes the pericardium and retains its relations with its primitive duct (which becomes the organ of Bojanus), and the other becomes filled with the gonadial products (eggs or sperm), and opens to the exterior by a duct (called the genital duct), which becomes constricted off from the primitive one. In the early stages of development of the mussel a pair of true nephridia, developed from the epiblast and with intra-cellular duct, is present, but it disappears later, when the primitive genital duct (peritoneal funnel of Goodrich) assumes a renal function.

[1] It is only right to say that the development of the renal gland in *Astacus* has not been fully observed, but it has in certain other Crustacea, and in all probability what is true of them is true of *Astacus*.

The genital ducts of the earthworm arise as peritoneal (cœlomic) outgrowths, which grow backwards from the genital pouches (seminal vesicles and cavity of the thirteenth segment) to the exterior; they are thus true genital ducts of mesoblastic origin. The nephridia are true nephridia, arising from the epiblast and growing *inwards* to the cœlom, with which they later in development communicate.

Thus, of the three cœlomate Invertebrates with which we are chiefly concerned, true nephridia are only present in one; the renal organ of the other two is a modified genital duct.

Among the Vertebrata, as we have already seen, the renal tubules of the pronephric and mesonephric system arise from the mesoblast; the pronephric tubules as outgrowths of the cœlom, and the mesonephric ones as solid strands, which become hollow, and in some cases communicate with the cœlom through nephridial funnels (nephrostomes). Zoologists have hitherto considered these tubules, at any rate the pronephric ones, as being homologous with the nephridia of worms, for like them they are primitively segmental, they are renal in function, tubular in form, and serve to place the cœlom in communication with the exterior. But they differ from true nephridia in that they are mesoblastic and not epiblastic in origin, and in that their lumena are inter-cellular and not intra-cellular. Their mode of origin, in fact, is like that of the genital ducts of the Invertebrata, and since we have seen that in them (crayfish and mussel) genital ducts may become renal in function, we are justified in tentatively assuming that the renal tubules of the pronephros and mesonephros of the Vertebrata are likewise modified genital ducts that have assumed a renal function. And such a conclusion is not so strange when we remember how intimate is the connexion between the renal and reproductive systems in them, for we have seen that the vasa efferentia are modified renal mesonephric tubules, and that the pronephric (Müllerian) and mesonephric (Wolffian) ducts become genital ducts, the former wholly, and the latter partly so.

But if this hypothesis of the primitively genital nature of the Vertebrate renal tubules be true, then the genital glands (gonads) of the primitive Vertebrates must have been segmental in nature, a pair in nearly every segment of the body, and communicating with the exterior through a pair of genital ducts. Now this is just the condition that we find in *Amphioxus*, where the gonads are developed in segmental genital pouches, the cavity of which is of cœlomic origin, and where every segment of the body, except the first few anterior

and posterior ones, contains a pair of gonads in the sexually mature animals.

Moreover it has been stated that the cœlom is a derivative of genital sacs [1]—of cavities in the wall of which the sexual cells are formed—and that among Invertebrata there are certain groups where the cœlom and the gonads are segmentally arranged; in others the cœlomatic cavities are segmental but the gonads are restricted to a few of them. Now, if it can be shown that the body cavity (cœlom) of Vertebrates arises as a series of segmental follicles, it will afford strong evidence in favour of the hypothesis that the gonads of Vertebrates were primitively segmental. And such is the case, for in *Amphioxus*, as already described, the cœlom arises as paired segmental evaginations of the archenteron or primitive gut, and in higher forms it arises as the excavation of mesoblastic blocks, the protovertebræ, segmentally arranged. The evidence is yet far from complete, but there is some reason for believing that the renal tubules, pronephric and mesonephric, arise as outgrowths of the cavities of these mesoblastic blocks (mesoblastic somites)—a pair of tubules from every pair of somites.

If such ultimately is demonstrated to be the case, then the homology of the Vertebrate renal tubules (pronephric and mesonephric) with Invertebrate genital ducts must be regarded as an established fact. And the pronephric and mesonephric ducts must be viewed as secondary acquirements formed in the course of phylogeny, as the result of the fusion of the outward extremities of the primitive genital ducts.

Another fact yet remains to be explained before such a hypothesis can be even provisionally accepted. It is this: if the renal tubules of Vertebrata are modified genital ducts which discharged their contents independently and directly to the exterior, is there any evidence that the pronephric and mesonephric tubules of Vertebrates ever possessed such a connexion? In them these tubules open, not directly and independently to the exterior, but indirectly and collectively through the pronephric and mesonephric ducts. In the first place then this connexion between the tubules and their duct is probably secondary, for the tubules invariably arise first and later assume their connexion with the duct. And secondly, it is now a demonstrated fact, that

[1] The student desirous of the evidence upon which this statement is made may obtain it in Goodrich's paper, published in the *Quarterly Journal of Microscopical Science*, XXXVII. 1895.

in Elasmobranchs—to which the dogfish belongs—and in mammals the pronephric tubules grow directly outwards until their distal ends reach the epiblast with which they fuse. This connexion with the epiblast lasts for a little while, and then a thickened ridge, extending backwards from tubule to tubule, begins to form. This thickening then extends backwards and ultimately reaches the cloaca; later it acquires a lumen, loses its epiblastic connexion, sinks into the mesoblast, and becomes the pronephric duct. We thus have, in this epiblastic connexion of the pronephric tubules, direct evidence that they once extended outwards to the skin, and by analogy, probably opened independently to the exterior. And further, in the ontogenetic development of the pronephric duct, we can gather some knowledge as to how it arose in the course of phylogeny.

Thus, as far as it goes, the evidence seems favourable to the hypothesis that the Vertebrate renal system has arisen as the modification of the metameric genital ducts of the primitive Vertebrate stock. But as yet it is a hypothesis; time and investigation can alone show whether it is to be advanced to the grade of a 'theory,' or to be relegated to the limbo where a great many other hypotheses have long since gone.

CHAPTER XVII

ORGANS OF RESPIRATION

THE organs of respiration among the Invertebrata, if we except *Balanoglossus* and the Tunicates, are of epiblastic origin; in some cases the general surface of the body acts as respiratory in nature, no definite organs existing for that purpose. In other cases they are epiblastic outgrowths, as in the crayfish and the mussel, and in others they are epiblastic ingrowths, as in the tracheæ of insects and the lung-books of scorpions.

Crayfish. In the crayfish there are three sets of gills, differing in their position. The first set arises as outgrowths of the thoracic epimera (Fig. 63) and are known as **pleurobranchiæ**; this set is very much reduced, only one functional pleurobranch existing on either side, in the last thoracic segment, while in the next two preceding segments there are a pair of vestigial gills, reduced to mere filaments.

The structure of the functional pleurobranch is the same as that of an arthrobranch to be next described.

The **arthrobranchiæ** are well developed, and arise as outgrowths of the arthrodrial membrane of the thoracic appendages (Fig. 63, AR.BR., AR.MEM). There are a pair of them for each thoracic appendage, except the first and the last, which have none at all, and the second (second maxillipede), which possesses a single one only. The two gills in each pair are so situated that one is anterior and the other posterior. Each gill consists (Fig. 80, E) of a **stem** (S), which is hollow, and internally is divided into two channels by a longitudinal septum (Fig. 63), which may be termed the **inner** and **outer channels**. The blood is propelled along the outer channel, thence into the inner channel, and thence into the branchio-cardiac canals (Fig. 63, BR.CAR.C), which open into the pericardium. In its course through the two channels of the stem, the blood traverses a spongy tissue contained in a number of **branchial filaments** (Fig. 80, G.F) that arise as outgrowths of the stem. It is while the blood is travelling through the branchial (gill) filaments, where it is separated from the external water only by the thin membrane of the filaments, that an interchange between the CO_2 of the blood and the O of the water is effected.

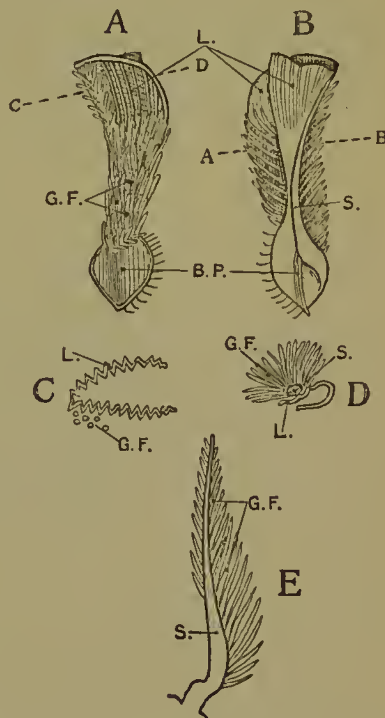


FIG. 80. The gills of the Crayfish (*Astacus*). A. Outer view of a podobranch. B. Inner view of a podobranch. C. Transverse section of a podobranch in the plane C—D. D. Similar section in the plane A—B. E. Inner view of an arthrobranch. B.P = basal plate; G F = gill (branchial) filaments; L = lamina; S = stem.

The **podobranchiæ** arise from the coxopodites of all the thoracic appendages except the first (first maxillipede) and the last (last ambulatory appendage). They are more complex in their structure than the arthrobranchiæ. Each consists of a **basal plate** (Fig. 80, A & B, B.P), arising from the coxopodite, and a **stem** (S), arising from its upper

border, and which terminates in a plate-like **lamina** (L). The lamina is doubled upon itself (Fig. 80, C), and is thrown into a number of corrugated folds; the object of the folding and doubling is doubtless to ensure a great increase of respiratory surface without increasing the bulk or size of the organ. From the stem there arise a number of **branchial (gill) filaments** (G.F). The blood follows the same course through the podobranch that it does through the arthrobranch, except that in addition it has the expanded lamina to traverse.

The three sets of gills lie in a **branchial chamber**, formed by the branchiostegites (Fig. 63) externally, and the thoracic epimeron (EP) internally. Through this chamber water is drawn from behind to in front by the sculling movements of the scaphognathite of the second maxilla, which lies in the **cervical canal**.

In the prawn-like crustacean, *Penæus*, all the pleurobranchiæ with the exception of the first are functionally developed, but all the podobranchiæ are reduced to mere plates, called epipodites, like the first one in the crayfish and the lobster. In crabs the gills are much more reduced, for among the podobranchiæ there is one on the second and third thoracic appendage only; with the arthrobranchiæ there is a pair on the third and fourth, and a single (anterior) one on the second; and there are only two pleurobranchiæ situated on the fifth and sixth thoracic segments; the first and the last two thoracic segments contain no gills at all. In lobsters there are as many podobranchiæ and arthrobranchiæ as in crayfishes, except that the second maxillipede bears no arthrobranch at all; there are four fully developed and functional pleurobranchs.

Cockroach. The organs of respiration in the cockroach consist of a number of anastomosing tubes that arise as infoldings of the epiblast. They are termed **tracheæ** or **tracheal tubes**, and commence at the **respiratory apertures** or **stigmata**, which are situated at the sides of the body, in the middle of each segment. They branch and anastomose with each other in a definite and constant manner, and traverse the blood-spaces and tissues of the body. Expiration and inspiration are effected by the alternate contraction and relaxation of the muscles of the body, which respectively compress and allow the elasticity of the tubal walls to expand the tubes; air is thus alternately forced out and sucked in.

Each tube is composed of a very thin wall of flattened cells, which secretes a spiral chitinous thickening along its inner surface, thus giving elasticity to the tube.

Fresh-water Mussel. The respiratory organs of *Anodonta* consist of two pairs, one on either side, of epiblastic fold-like outgrowths of the body-wall, which hang down into the infrà-branchial chamber. These folds, called **gills**, extend along nearly the whole length of the animal (Fig. 72, OG., IG). Each gill is double, consisting of two layers, called the **outer** and **inner lamellæ** (Fig. 72), which are fused with each other along their ventral margins; each gill thus encloses a cavity, and may be regarded as a somewhat elongated, narrow bag. The outer lamella of the outer gill of either side (O.G) is attached to the mantle along its whole length, but its inner lamella and the outer lamella of the inner gill are attached to the body-wall, as is also the inner lamella of the inner gill in its posterior half.

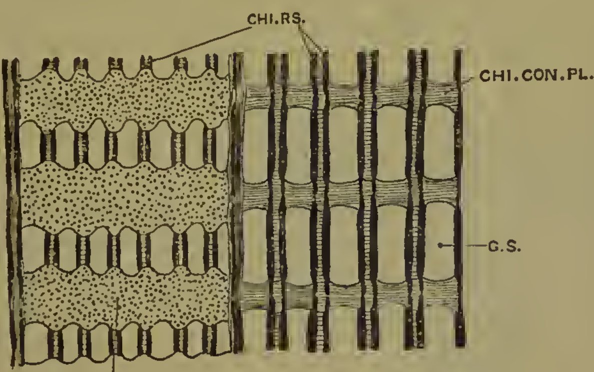


FIG. 81. Surface view of a small portion of the gill of *Anodonta* (Fresh-water Mussel). In the half to the left hand the epithelium has been brushed away from the chitinous (skeletal) rods, while in that on the right hand all the epithelium has been so brushed away, in order to show the entire skeletal part. CHI.RS = chitinous (skeletal) rods; CHI.CON.PL = chitinous plates connecting skeletal rods; EPI = epithelium; G.S = gill-slits.

Each lamella is supported by a number of minute, vertically arranged, chitinous rods (Fig. 81, CHI.RS), between which there are slit-like perforations (G.S), which place the cavity of the infra-branchial chamber in communication with that enclosed between the two gill lamellæ. The chitinous rods are joined together by chitinous plates (CHI.CON.PL), above and below each gill-cleft, and the whole is covered with a columnar or cubical, ciliated epithelium (Fig. 82, EPI and Fig. 81, EPI). At intervals the outer (O.LA) and inner (I.LA) lamellæ are joined together by connecting strands, termed the **inter-lamellar junctions** (Fig. 82, IN.LA.J). Within each lamella there are a number of anastomosing, spongy-like cavities, containing blood (Fig. 82, BL.SIN), some of which pass from one lamella to the other;

the greater portion of the space between the two lamellæ is, however, a water-channel, and is in free communication with the infra-branchial chamber through the gill-clefts (Fig. 82).

The blood, contained in the blood sinuses, is thus separated from the oxygen-containing water only by a thin membrane (Fig. 82), composed of a single layer of cubical cells; and while the blood is slowly travelling through these sinuses it is exchanging its CO_2 for some of the O of the water.

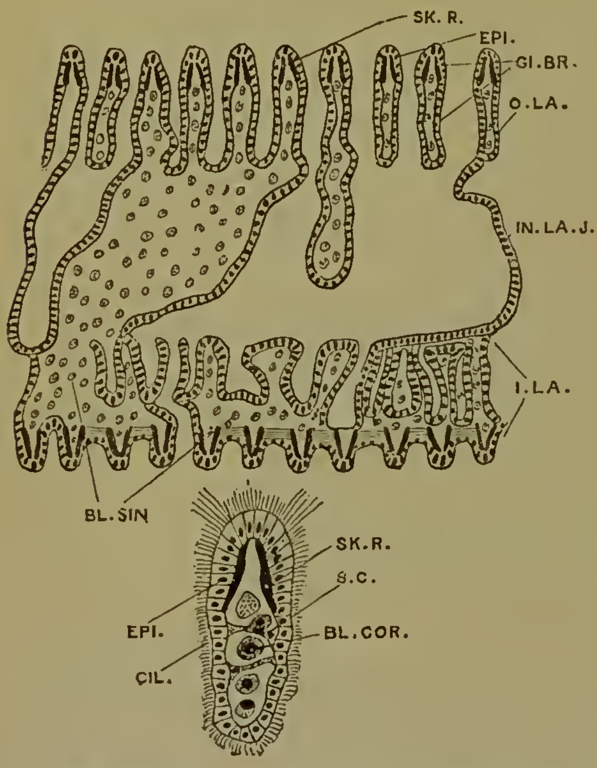


FIG. 82. Portion of a transverse section of the gill of *Anodonta* (Fresh-water Mussel), taken in a plane at right angles to the chitinous rods (Fig. 81). BL.SIN = blood sinus, containing blood corpuscles; BL.COR = blood corpuscle; CIL = cilia; EPI = epithelium; GI.BR = gill bar; I.LA = inner lamella; IN.LA.J = interlamellar junction; O.LA = outer lamella; S-C = supporting cell of branchial bar; SK.R = skeletal (chitinous) rods. The small figure below the larger is a single branchial bar as seen under the one-sixth objective. The inner lamella shows the appearance of a section that passes through the plane of the connecting chitinous plates (CHI.CON.PL, Fig. 81), while the outer lamella shows that of one which passes in the plane of the gill-clefts (G.S).

Along the dorsal margin of each gill the cavity contained between the two lamellæ is slightly enlarged, and forms a tubular canal that runs backwards along the length of the gill to the cloacal chamber; these canals are the **supra - branchial chambers.** Hence water passing into the infra-branchial chamber through the inhalent aperture (Fig. 72, I.A & I.B.C) has two paths by which it may travel: the greater portion passes through the gill-slits into the cavity between the gill-lamellæ, thence to the supra-branchial chambers, whence it is carried to the cloacal chamber, and then expelled to the exterior through the

exhalent aperture (Fig. 72, E.A); the smaller portion travels forward to the mouth, and reaches the alimentary canal, through which it passes until it reaches the rectum (R), when it is poured into the cloacal chamber (C.C), and thence to the exterior. Thus of the stream of water passing through the inhalent aperture, part becomes respiratory in value and the other nutritive.

In the figure (72) a long rod terminated by an arrow is placed in each supra-branchial chamber, and inspection will show that the renal (R.A) and genital (G.A) apertures open into the supra-branchial chamber of the inner gill, so that the outflowing stream of water carries away to the exterior the renal and genital products.

The supra-branchial chambers of the two inner gills are separated in the region of the visceral mass, but from behind this to the cloacal chamber they are confluent; so that in this latter region there are three and not four supra-branchial chambers, i. e. a median one representing the confluent chambers of the two inner gills, and, on either side, the chamber of each outer gill.

The direction of the flow of the water is determined by the cilia which line the branchial chambers and the cavity of the alimentary canal, and which clothe the surface of the gills.

Earthworm. There are no definite respiratory organs in the earthworm, and respiration probably occurs over the whole surface of the body; the exceptional fact that the blood capillaries actually penetrate between the epidermal cells would greatly facilitate such a function.

CHAPTER XVIII

ACŒLOMATA-INVERTEBRATA (DIPLOBLASTICA)

THE MORPHOLOGY OF HYDRA.

Hydra differs from all the animals we have hitherto considered in the absence of a cœlom or body cavity, and of a middle germinal layer, the mesoblast, or its adult equivalent the mesoderm. Considered in a general way *Hydra* is a double-layered sac, the cavity of which is a digestive one; the inner layer which lines this cavity is the equivalent of the endoderm (embryonic hypoblast), and the outer layer is the homologue of the ectoderm (embryonic epiblast) of the Cœlomata. Thus, so far as its fundamental plan of structure is concerned, it may

be regarded as a permanent gastrula stage of the higher forms of life. The term **diploblastica** is applied to all animals which, like *Hydra*, consist of two layers only, in order to distinguish them from those of the **triploblastica**, in which a middle mesoderm is added. It is interesting to note that the lower Metazoans are diploblastic, and the higher triploblastic; and, among the latter, the lower forms of these are acœlomate, while the higher are cœlomate. In the course of the development of a cœlomate Metazoan its earlier stage is a diploblastic one, the epiblast (ectoderm) and hypoblast (endoderm) only being present; later the mesoblast (mesoderm) appears, and the organism is then at the triploblastic-acœlomate stage, and later still, by the appearance of a cœlom, it becomes a triploblastic cœlomate. Thus the ontogenetic development of one of the higher forms passes through, in the proper sequence of events, the evolutionary stages that are indicated by the study of comparative anatomy; so that, as will be insisted upon in another chapter, an organism's development is a recapitulation of its evolution.

Hydra is a fresh-water form inhabiting slowly-running streams and ponds, and usually adhering to some floating object such as weeds, twigs, or leaves. It is very easy to keep under observation in a glass vessel, in which a little green weed like the Canadian water-weed is placed, throughout the whole of the spring, summer, and autumn. Watched under these circumstances it can be seen that the organism is cylindrical in form, and attached by one extremity to some object. At the other extremity it bears a number of extremely small, filamentous bodies, just visible to the unaided vision, and called **tentacles** (Fig. 83, TEN). The tentacles and the body are continually changing their form, sometimes elongating to such an extent that they become barely visible, and at other times contracting into a small knob-like body. Within the circle of tentacles there is a conical eminence called the **hypostome** (HY), at the summit of which is the circular aperture of the **mouth** (M).

Hydra feeds mainly upon minute crustaceans like water-fleas, which, in their rapid and apparently indiscriminate movements through the water, sometimes come into contact with the tip of one of the expanded tentacles. If the animal be hungry, the movement of the water-flea is arrested by the discharge into it of a poisonous fluid formed by the **stinging batteries** (Fig. 83, S.B). The arrest and subsequent ingestion of the water-flea is rendered more certain and effectual by the convergence of the other tentacles upon it, which, having sufficiently

paralysed its movements, bend inwards and thrust it through the aperture of the mouth into the **gastric cavity** or **enteron** (ENT). Here it undergoes digestion of its soluble portions, the insoluble remnant being thrown out again through the mouth. The mouth thus serves additionally as an anus.

Three species of *Hydra* are very commonly found: *H. vulgaris* is a colourless form; *H. fusca* is brownish in colour; and *H. viridis* is green. The colour in the last two species is due to coloured granules lying in the inner layer, for under the low power of the microscope it can be easily seen that the whole animal is invested externally in a colourless layer.

During the spring and summer *Hydra* can be seen to bear one or more small hydra-buds upon it; and very often these little buds bear other buds, so that temporarily a little colony is formed. These are vegetative outgrowths of the body-wall, and as soon as they have attained a certain size they become constricted off from the parent as an independent individual. Each bud arises at first as solid proliferations of the epiblast, but very soon the hypoblast and enteron push into it, so that it is of the form of a hollow outgrowth. Tentacles then grow out from its free extremity and a mouth is formed. It then becomes constricted off at its base from the parent. Thus, during the spring and summer, *Hydra* reproduces rapidly by the formation of asexual buds; this is termed **agamogenesis**. But in autumn, when the temperature begins to fall and food material becomes scarce, it resorts to reproduction by sexual means or **gamogenesis**. At this period two little eminences appear upon the surface of the body, one being conical in form and situated in the upper part just behind the ring of tentacles, and the other lower down and somewhat rounded in form. The upper one is the **testis**, and the lower one the **ovary**. The **ovum** or **egg** becomes fertilized and undergoes an immediate preliminary development, by which the embryo becomes encased in a hard investment, and then it sinks to the bottom of the water, where it remains dormant until the early spring of the next year.

When transverse sections across the body of the animal are examined, it is seen that it contains a central cavity (Fig. 83, B, ENT) surrounded by two layers, an inner **endoderm** (EN), and an outer **ectoderm** (EC). Between these two layers there is a thin, structureless, jelly-like film, called the **mesoglœa**, indicated in Fig. 83, C, by a black line just within the index line of KF. It foreshadows the mesoderm of the triploblastica, and in some other of the Hydrozoa it

even exhibits an incipient cellular structure, due to the presence within it of what are probably migratory cells.

The **ectoderm** is not a simple layer of cells, but consists of several constituents. The largest of these cells are pyramidal in form (Fig. 83, B, C, D, EC.C), with their bases directed outwards; they are called the **ectoderm cells.** Each contains a nucleus (NC), and its free surface is marked by a vertical striation, to which the name **striated free-border** is given. It probably represents the last remnants of cilia, for *Hydra*, and another hydrozoön, *Tubularia*, are exceptional

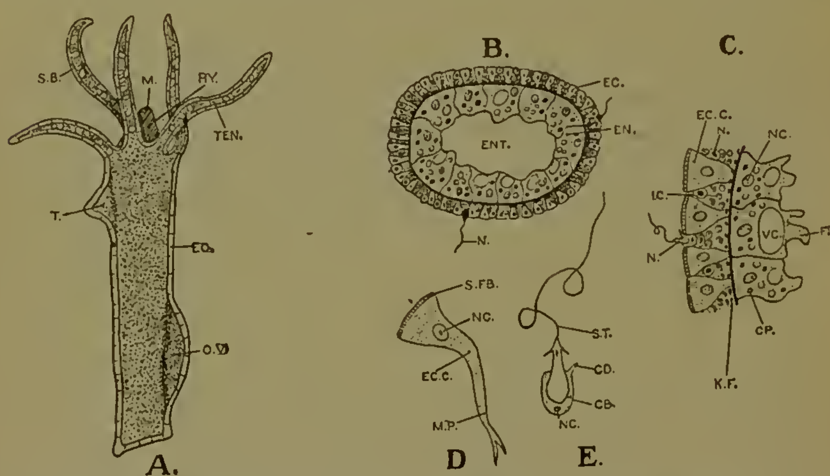


FIG. 83. A. External view of *Hydra*. B. A transverse section of the same seen under a two-third objective. C. A portion of B seen under the one-sixth objective. D. An ectoderm cell separated from its fellows by maceration in potassium chromate. E. One of the stinging organs. CB = cnidoblast; CD = cnidocil; CP = chromatophore; EC = ectoderm; EC.C = ectoderm cell; EN = endoderm; ENT = enteron or digestive cavity; F = flagella; HY = hypostome; I.C = interstitial cells, forming a syncytium; K.F = Kleinenberg's fibres (neuro-muscular processes M.P of the ectoderm cells); M = mouth; N = nematocyst; NC = nucleus; OV = ovary; S.B = stinging batteries; S.FB = striated free-border; S.T = stinging-thread; T = testis; TEN = tentacles; VC = vacuole.

among the class, in that they do not pass through a free-swimming, ciliated, blastula stage, for at this stage in their development they are quiescent. The inner end of the cell is prolonged into a fibrous process, which extends downwards along the outer surface of the mesoglœa; since these processes extend downwards from every ectoderm cell, it follows that in a transverse section they will be seen cut across, lying immediately outside the mesoglœa. They were first described by Kleinenberg, and were formerly known as **Kleinenberg's fibres** (K.F); more recently they have been named **muscular fibres** on account of the fact of their contractile nature; and some regard

them as being both muscular and nervous in nature, and speak of them as the **neuro-muscular fibres**. It is due to their contraction that the various movements of the animal are originated.

Occupying the spaces between the apices of the pyramidal ectoderm cells are a number of smaller ones, called the **interstitial cells** (Fig. 83, C, I.C). The protoplasm of the individual cells runs together, so as to form a continuous jelly in which the nuclei are scattered; such a fusion of the protoplasm of cells is called a **syncytium**, and is very characteristic of sponges. Among the interstitial cells certain vesicles may be noticed; these are developing **nematocysts**, and as their development becomes completed they are gradually carried outwards by the migratory movement of the parent cell, called a **cnidoblast**, in which they arise. A fully formed nematocyst is shown in Fig. 83, E. The nematocyst is a flask-like vesicle, prolonged outwards into a delicate filament, the stinging-thread (S.T). At the neck of the nematocyst are some recurved barbs, probably instrumental in injecting an irritant poison into the prey. The nematocyst is enclosed in a cell with a nucleus (N); this cell is derived from one of the interstitial cells, and is the parent cell of the nematocyst; it is hence called a **cnidoblast** (CB). It is prolonged outwards into a little process called the **cnidocil** (CD) or trigger-hair, which is thought to be extremely sensitive to external stimuli, and to bring about contraction of the protoplasm of the cnidoblast. In the undischarged state the stinging-thread is coiled away or inverted within the nematocyst; its discharge is brought about by its eversion when the nematocyst is pressed upon by the contraction of the cnidoblast. Very frequently the cnidoblast is seen to be in communication with branched stellate cells having a large nucleus; these are probably **nerve cells**, and they occur dispersed over the outer surface of the mesoglœa, constituting a diffuse and rudimentary nervous system. They belong to the ectoderm layer, and we have already seen that the highly concentrated nervous system of higher forms also arises from this layer, and secondarily becomes embedded in the deeper mesoblast.

Along the tentacles the nematocysts are aggregated in groups, called the **stinging batteries** (Fig. 83, S.B).

Two other but simpler forms of nematocysts also exist; they are very small, and both sorts consist of a vesicle, but the one has a short, straight and tapering thread, and the other a coiled one.

The **endoderm** is composed of a single layer of large, flagellated

cells. They are characterized by the possession of large vacuoles (Fig. 83, VC), which are formed by the running together of small droplets; the fluid contained within them is probably discharged into the enteric cavity (ENT) as a constituent part of the digestive fluid. In addition to its nucleus (NC) the cells contain certain small, rounded bodies (CP) called **chromatophores**. In *H. fusca* they are brown in colour, and the colour of the animal is due to their presence; in *H. viridis* they are coloured green with chlorophyll, and, when extracted from the endoderm cells, have been observed to reproduce themselves, so that probably they are unicellular algæ. Other smaller granules, black and brown in colour, are present in the endoderm cells, and probably represent the degeneration products of the chromatophores, or they may be excretory in nature.

Muscle-processes, running in a circular direction, are connected with the endoderm cells, and their contraction reduces the size of the animal circumferentially, while the contraction of those of the ectoderm shortens it in its length.

Among some of the ordinary endoderm cells there are to be found at the end, near the tentacles, certain elongated cells with very granular protoplasm. The possession of a granular protoplasm by cells is indicative of a secretory activity, that is, of the formation of some substance that is destined to play some useful part in the living economy. In this particular instance the granular substance formed within these narrow cells is probably of the nature of a digestive ferment which, when it is discharged into the gastric cavity, becomes dissolved in the fluid liberated from the vacuoles of the ordinary cells, the two together forming a digestive juice. A **ferment** is a body which, while it is capable of exciting changes in other bodies, does not itself undergo change.

A water-flea, or other particle of food substance, when taken into the gastric cavity of *Hydra*, undergoes the process of digestion; that is, the insoluble material of which it is composed is rendered soluble, so that it is capable of filtering through the tissues of the *Hydra*. In addition to this digestion in the gastric cavity the endoderm cells appear to have the power of taking up minute particles of food by means of their flagellæ, and ingesting them into the substance of their protoplasm, there to digest them, very much as the unicellular *Amœba* does. In *Hydra*, therefore, we may distinguish between an **intra-cellular** digestion, which takes place within individual cells, and an **inter-cellular** one, which occurs between or among an aggregate of cells.

The endoderm is thus an entirely digestive layer, concerned only with the formation of the digestive juices. The food substance rendered soluble and diffusible is absorbed by it, and passed on by osmosis to the ectoderm. By all the cells of the animal this is acted upon and converted into living protoplasm; in other words, it is assimilated. And the result of this assimilation is growth until the organism attains the limits of size set upon its species, when continued growth then assumes the form of reproduction in the production of bud-like outgrowths that ultimately become constricted off from the parent. Thus reproduction may be looked upon as a process of continued growth, or as one that, while preventing the overgrowth of the individual, ensures the continued growth of the race.

The organs of sexual reproduction arise, in the positions already indicated, from some of the interstitial cells. Both testis and ovary are formed upon the same animal, so that *Hydra* is **hermaphrodite.**

The **testes** (Fig. 83, T) are usually only few in number, and arise from a little heap of interstitial cells, which are covered by the larger ectoderm cells that are somewhat more flattened than the ordinary ones. Each interstitial cell becomes a **spermatozoön**, a small, filamentous body with a minute ovoid head at one end; its tail is vibratile, and by the rapid movements of this it is carried through the water.

The **ovaries** (OV) are larger than the testes, and like them at first consist of a little heap of interstitial cells. One among these grows bigger than the rest, becomes amœboid, and develops yolk-granules within its substance. By means of its amœboid pseudopods it ingests the surrounding interstitial cells, and grows very big at their expense. When mature it assumes a spherical form, and becomes invested by a layer of interstitial cells. The large cell is the **ovum**, and the investing ones the capsule. After a while the capsule bursts and liberates the ovum, which creeps about by amœboid movements at the bottom of the water; sooner or later it may become fertilized by the entry of a spermatozoön.

Immediately after fertilization the **oosperm**, as the fertilized ovum is called, divides up into a number of cells which form a solid mass, there being no central cavity (segmentation cavity) around which they are arranged, as is usually the case. The outer layer of these cells becomes converted into a chitinous membrane, and in this condition, which takes about four days to attain, the embryo remains quiescen

for a period of from six to eight weeks. The cells then fuse together, and in the centre of the protoplasm a space begins to appear. This gradually gets larger, and ultimately forms the gastric cavity. A distinction into a relatively clearer ectoderm and a slightly more granular endoderm then becomes visible, and the mouth begins to appear by a thinning of the wall at one pole of the embryo. At this thin point a rupture appears and the mouth is formed ; simultaneously with which the tentacles arise as hollow outgrowths of the gastric cavity. At about the time that the gastric cavity first appears the outer chitinous layer is ruptured and thrown off, and the embryo then moves freely in the water.

The development of *Hydra* is not typical of the class to which it belongs, for the normal course of development consists in the formation of a hollow ball of cells (**blastosphere**) from the oosperm ; the wall of this consists of a single layer of cells, and from its inner surface a number of cells are budded off, which by division soon fill up the cavity of the blastosphere. The outer layer of cells is the epiblast layer, and the central mass is the hypoblast. Within this latter a cavity soon appears which forms the rudiment of the gastric cavity. The whole embryo then elongates and becomes covered externally with a covering of cilia, by means of which it swims about in the water. This stage is known as the **planula stage**. Later it comes to rest, and a mouth and tentacles appear.

Thus the development of *Hydra* is abnormal, in that it modifies the blastosphere and suppresses the free-swimming planula stage. In other words, it abbreviates its development.

When dealing with the endoderm layer we called attention to the fact that there was reason for regarding the green chromatophores as unicellular algæ. There thus exists a combination of an animal and a plant living together. The meaning of this is not far to seek, for among the activities of plants that of utilizing the carbon of the CO_2 of the atmosphere and returning half of the oxygen plays an important part ; while among those of animals that of using the oxygen of the atmosphere and giving CO_2 in return is no less important. Hence in such a combination the animal's waste is the plant's food, and that which the plant throws off is used for the respiration of the animal. The two organisms thus live together for the mutual benefit of both, forming a kind of co-operative arrangement. In biological language this is known as **symbiosis**.

Symbiosis differs from **parasitism** in that the presence of neither

organism is detrimental to the other. In parasitism one organism thrives at the expense of the other, living upon its tissues.

Commensalism is another partnership of two organisms in which, while the one organism alone derives benefit from it, the other suffers no harm from the association. The 'beef-eater' bird, for instance, lives in close association with cattle, perching itself upon their backs and extracting the grubs from their skins. There is a certain little marine fish which lives inside a large sea-anemone, and, while the fish does not harm the anemone, it benefits by living upon some of the food of the latter.

CHAPTER XIX

PROTOZOA

The Morphology of Paramœcium and Amœba.

All the animals we have so far studied, with the exception of *Hydra*, are composed of a complex arrangement of organs each fulfilling a definite function, and each composed of several tissues, which in their turn are aggregates of cells. In *Hydra* the morphology of the organism is so simple that it is composed of only two tissues, arranged in two layers, and which perform between them all the functions of life. In the Protozoa the morphological organization is still simpler, and in fact is almost as simple as it is possible to conceive, for every Protozoan is a simple morphological and physiological unit; that is to say, it consists of a single cell. Some of them in the course of their life-history (ante, p. 27) run together and form a continuous mass or branching strand of protoplasm with numerous nuclei embedded in it, and so far resemble a multicellular organism. But the course of their life-history reveals their true nature, for at no period do they pass through those definite embryological stages, such as the blastula and gastrula, which even the simplest Metazoan does, and neither do they exhibit a morphological and physiological differentiation of their cells into tissues.

Although no morphological—that is to say a structural—differentiation can be discerned among the Protozoa, a chemical and physical differentiation is exhibited of the protoplasm of which the individual is composed. And dependent upon a differentiation of this sort the Protozoa have been divided into two groups: the **Gymnomyxa** and

the **Corticata**. The former group includes those animals which, like *Amœba*, live throughout the whole or greater part of their life as a naked mass of protoplasm, and which are capable therefore of ingesting food particles at any part of their body. The latter group includes those forms which, like *Paramœcium*, have the outer layer of protoplasm physically differentiated, so that it is denser and firmer than the central mass; one result of this is that the body form is constant, and that food particles must be taken in at definite parts of the surface where the protoplasm remains soft.

The Gymnomyxa are divided into seven classes, and one of these is called the **Lobosa**. This class is characterized by the fact that the organisms grouped in it exhibit amœboid movements during the whole or the greater part of their life, and that the pseudopods, in virtue of which the amœboid movement is exercised, are lobose, thick and blunt in form, never filamentous and never fuse together, as in the class **Reticularia**. To the class **Lobosa** *Amœba* belongs.

The Corticata are divided into six classes, among which is that of the **Ciliata**. The special feature of the organisms belonging to this class is the possession of cilia, either arranged in rings or more uniformly diffused over the whole surface. It is further divided into four orders: the **Peritricha**, **Heterotricha**, **Holotricha**, and **Hypotricha**, according as the cilia is arranged in rings, or the body is covered uniformly with short cilia with a circle of long cilia round the mouth, or it is arranged uniformly in lines over the surface of the body with no additional circlet, or it uniformly covers only one surface (ventral) of the body. *Paramœcium* belongs to the Holotricha.

PARAMŒCIUM.

Paramœcium may be obtained with certainty in an infusion of hay, or from water in which flowers have been standing for several days. It is known under another name, that of the 'slipper animalcule,' on account of its form. It is just visible to the unaided eye as a whitish speck, and measures about $\frac{1}{5}$–$\frac{1}{4}$ mm. (200–260 μ) in its longest diameter. It is bluntly rounded at one end (Fig. 84) and more tapering at the other. The blunt end is carried forward as the animal moves, and it is hence called the anterior end, and the other will therefore be the posterior end. Upon the flattened surface that is usually carried face downwards as the animal moves, and which is therefore on the ventral surface, there is a shallow depression leading

from the left side of the body inwards to the under surface; this is the **buccal groove** or **vestibule** (V). It is wide where it begins at the side of the body and narrows somewhat as it passes to the ventral surface; it is continued inwards, passing through the outer and denser protoplasm into the softer central portion; the inward, tubular, continuation of the groove is called the **œsophagus** or **gullet** (Œ), and is lined with a thin cuticular secretion of the protoplasm.

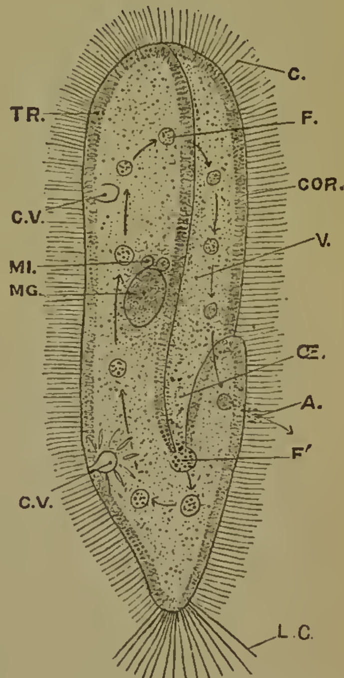


FIG. 84. *Paramœcium* (Slipper animalcule). Viewed from the ventral surface. A = anal spot; C = cilia; C.V = contractile vacuole; COR = cortex; F = food particles in a vacuole of digestion; F′ = food particles in the vacuole of ingestion; L.C = tuft of long cilia; MI = micronucleus; MG = meganucleus; Œ = œsophagus or gullet; TR = trichocysts; V = vestibule or buccal groove. The arrows indicate the direction of the movement in the circulation of the food vacuoles

Careful observation of its movements shows that its form, though perfectly flexible, is permanent and constant. This permanency of outline is due to the presence of a secreted cuticle, similar to that lining the gullet, and of tolerably firm consistency. Within this cuticle the protoplasm is obviously differentiated into an outer denser, fibrillar-marked **cortex, cortical layer,** or **ectosarc** (Fig. 84, COR), and an inner more fluid **medullary portion, endosarc** or **endoplasm.**

Arising from the cortical layer, and passing out through perforations in the cuticle, are numerous, uniformly sized, cilia (C), arranged in lines parallel to the long axis of the body. In certain species the cilia at one or both ends are slightly longer than the rest (L.C). The cilia pass down along the **vestibule** or **buccal groove** (V), and, like those over the rest of the body, are in continual motion; the action of the cilia is such that food particles are wafted from all sides down into the gullet, where they collect at the bottom, and form a ball (F′).

As soon as the ball of food material reaches a certain size it is jerked off into the medullary protoplasm, and becomes surrounded by a fluid secreted by the protoplasm. It thus lies in a vacuole, and in this it is carried round in the circulating protoplasm in the

direction indicated by the arrows in the figure. In *Paramœcium bursaria* it has been observed that the circulation is completed in $1\frac{1}{2}$ to 2 minutes, which gives a rate of rotation of $\frac{1}{9000}$ to $\frac{1}{12000}$ of an inch per second. While travelling round in the endoplasm (medulla) the food particles undergo digestion, and ultimately nothing but the insoluble portion of the food remains; this is ejected to the exterior at a constant point in the protoplasm, which may be called the **anal spot** (A). For the sake of convenience we may distinguish between a vacuole of ingestion, one of digestion, and one of egestion.

The cortex is fibrillated in a direction perpendicular to the surface, and is beset with innumerable, small, oval bodies, which, when the animal is irritated, shoot out into long filaments, and have been termed the **trichocysts** (TR). They are probably of the nature of stinging-threads. In *P. bursaria*, green granules of chlorophyll occur in this layer.

Lying in the cortex there are two **contractile vacuoles** (C.V), one at about a third the distance from either end. They have received this name because they alternately dilate and contract. If we watch one of them, it will be seen that its position is constant, and that it gradually increases in size and radiating canals appear round it (lower C.V); suddenly the vacuole contracts and disappears completely, but almost immediately afterwards the canals run together and form the beginning of another vacuole, which begins to dilate and passes through the same changes. The period of dilation is called the **diastole** and that of contraction the **systole**. There is not much doubt but that they are excretory in nature, getting rid of the nitrogenous waste and of the water ingested with the food particles. In *Amœba*, as we shall presently see, the presence of nitrogenous bodies in these vacuoles has been experimentally demonstrated.

Embedded in the endoplasm (medulla) at its junction with the cortex is an ovoidal body that stains with a uniform tint when treated with nuclear dyes, and which does not show any distinction into chromatin and achromatin (post, p. 352), such as is usual in nearly all nuclei. Lying near it are two much smaller bodies, which do not stain in the same way and show chromatin elements. The larger nucleus is called the **meganucleus** or **macronucleus** (MG), and the smaller ones the **micronuclei** or **paranuclei** (MI). In some species (*P. caudatum*) there is only one micronucleus.

Reproduction. *Paramœcium* reproduces asexually and sexually. The asexual reproduction is a very rapid one, and by its means the

number of *Paramœcia* may be very rapidly increased. It consists in the simple transverse fission of the cell into two parts, the cell division being preceded by the elongation and division of the meganucleus and micronuclei. The former divides directly, but the latter undergoes a definite mitosis (post, p. 352).

Agamogenetic division cannot go on indefinitely, for it has been demonstrated in the case of other Protozoa that after vegetative fission has been repeated a certain number of times the resulting progeny become dwarfed; and if this process were repeated they would ultimately disappear. Hence it is apparently necessary that now and then the vitality[1] (using this word for the want of a better one) of the protoplasm should be revived or stimulated by the union with it of another and similar mass.

The sexual reproductive process in *Paramœcium* is of the simplest expression of that process, and yet owing to the method by which it occurs it is in reality somewhat complex. Two *Paramœcia* apply themselves by their ventral surfaces (Fig. 85, 1), and then the two micronuclei (MI) in each divide into two (2). This is again repeated, so that there are at this stage eight micronuclei in each individual (3). At about this stage the meganucleus (MG) becomes mammillated, and seven (MI′) of the eight micronuclei begin to disappear. The single micronucleus that persists enlarges and then divides into two (4); of these, one remains stationary and is called the **female pronucleus** (4, F.P), but the other migrates over into the other individual and is called the **male pronucleus**. During these changes the meganucleus begins to break up. The male pronucleus that migrated from either one of the conjugating pair then fuses with the female pronucleus of the individual organism into which it passed and forms the **conjugation nucleus** (5, C.N). At the same time the fragmentation of the meganucleus is continued, and it is now broken up into a number of fragments (MG). In the next phase the seven parts (MI′) derived from the division of the micronuclei almost completely disappear (6), the meganucleus becomes more fragmentary, and the conjugation nuclei begin to divide into two (6, C.N′). And at about this time the two individuals separate from one another. In the next phase the fragments of the meganucleus begin to disappear, probably being extruded, and the conjugation nuclei divide into two, one of the two portions

[1] Let the student beware of assuming that the word 'vitality' has any real meaning. It is merely a mask by which we clothe our ignorance of the ultimate nature of life.

passing to one end, and the other to the other end of the organism (7, C.N′). Each portion then divides again, so that there are two at either end (8). Of these, the two at the posterior end (9, MI″) undergo no change, and become the micronuclei of the new individuals, while

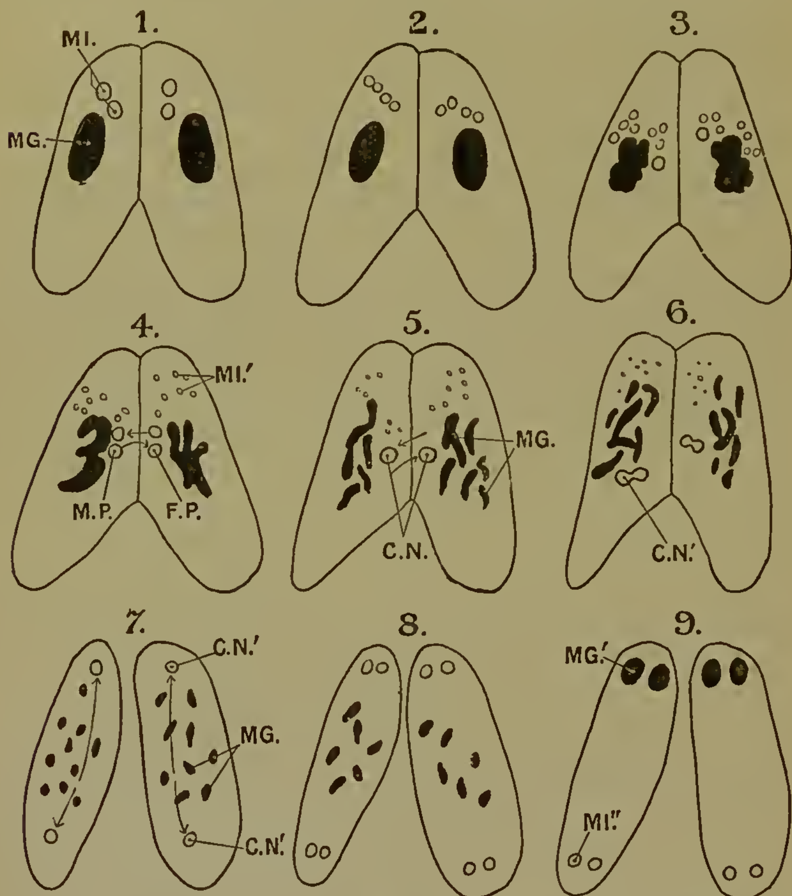


FIG. 85. *Paramœcium aurelia.* The processes concerned in conjugation, slightly diagrammatically represented. (Based upon Maupas.) C.N = conjugation nucleus; C.N′ = the nuclei derived from the division of the conjugation nucleus; F.P = female pronucleus; MI = micronuclei; MI′ = products of micronuclear division in course of disappearing; MG = macronucleus in 1, 2, and 3, and fragments of it in the remainder; MG′ = the new macronucleus; M″ = the new micronuclei; M.P = male pronucleus.

those (MG′) at the anterior end enlarge and become the meganuclei of the two offspring. By this time the whole of the fragments of the original meganucleus have disappeared. In some species (*P. caudatum*) some of the fragments possibly contribute towards the formation of the new nucleus.

Thus in each of the two individuals partaking in the act of conjugation there are now two meganuclei and two micronuclei. Each individual now divides in a longitudinal plane, and each of the two micronuclei divide again. So that from the original two *Paramœcia* there are derived four individuals.

The fundamental act in the whole series of these complex changes is the fusion of the male pronucleus of one individual with the female pronucleus of the other. But as far as it is possible to ascertain, the male and female pronuclei are identical, unless the fact that one migrates while the other remains stationary can be considered a difference of any importance. There is, therefore, apart from this act of migration, no differentiation into a male spermatozoön and a female ovum, such as is the case in *Hydra* and in all the other animals we have considered. And there are reasons for regarding this phenomenon of the fusion of identical masses, but derived from two individuals, as a rudimentary sexual act; that is to say, that in some such way as this sexual reproduction first arose. And we speak of this act as one of **conjugation** in order to distinguish it from that definitely sexual one where the male element can be distinguished from the female in virtue of its size, form, and movements.

AMŒBA.

Amœba or the Proteus animalcule is a microscopic organism measuring on an average about the $\frac{1}{100}$ inch in diameter. It is usually found in stagnant water adhering to weeds or submerged plants, or creeping in the mud at the bottom of the pond.

Examined under the high powers of the microscope it is seen to consist of a shapeless and ever-changing blob of jelly-like substance (Fig. 86); this material is living **protoplasm** in its simplest and most easily examined form. The student will do well to examine it with great care and at leisure, and endeavour to understand for himself what life is like in its simplest manifestation. The blob of protoplasm is colourless, and the greater portion of it is finely granular (EN); some of the granules are larger than others, and probably have a significance different to that of the others, for they may be living while the others are possibly dead. On the outside of the granular portion is an extremely thin layer of clear protoplasm (EC) that is very easily overlooked. The central granular part is termed the **endosarc** or **endoplasm** (EN), and the clear, hyaline investing film, the **ectosarc** or **ectoplasm** (EC).

Embedded in some portion of the endosarc is an ovoidal body, the **nucleus**. This consists, in most species of *Amœbæ*, of an investing **nuclear membrane**, containing a colourless and unstainable **nuclear sap**, sometimes called the **achromatin**, embedded within which are certain granules or strands of material that stain deeply, and are collectively called the **chromatin**. The chromatin substance is differently arranged in the nuclei of different species, but is constant for the individuals of the same species.

If an *Amœba* be watched in a drop of water upon a slide under the microscope, it will be seen that its form is continually changing, by

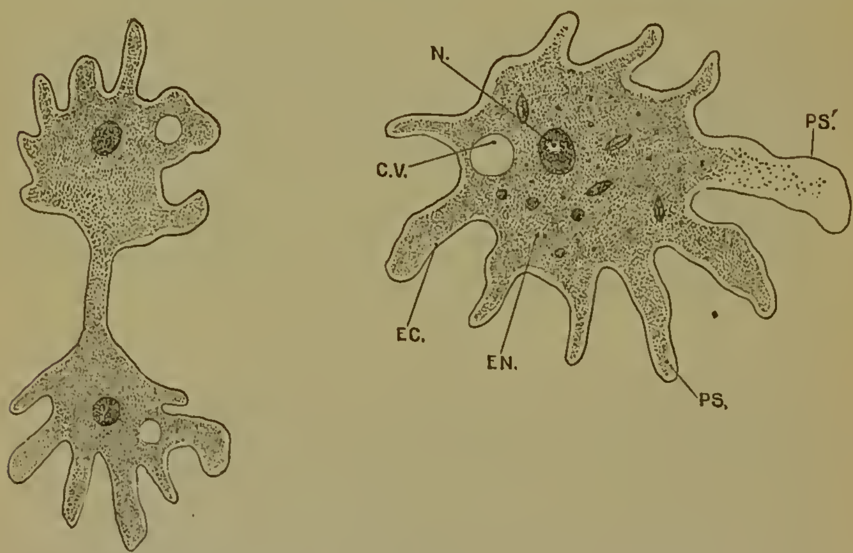


FIG. 86. The figure on the right shows an *Amœba* as it is to be seen crawling on the slide, while that on the left represents one in the act of dividing into two. C.V = contractile vacuole; EC = ectoplasm or ectosarc; EN = endoplasm or endosarc; N = nucleus; PS = pseudopod; PS′ = a pseudopod in the course of formation; the ectoplasm is first protruded, the endoplasm subsequently flowing into it.

the projection at one point and the retraction at another of blunt processes or **pseudopoda** (Fig. 86, PS). The size and rapidity of movement of these vary in different species; in some they are mere papilla-like projections of the protoplasm, and the alteration in the form of the body is almost imperceptible; in others they are elongated and almost filamentous, and are protruded and retracted with relatively great rapidity, so that the organism exhibits a kind of restless movement, and is continually moving from one part to another. Between

these two extremes intermediate forms, such as that figured, are to be found.

Locomotion is effected by the protrusion of a pseudopod and the flowing of the body after it. When first protracted, a pseudopod consists of nothing but ectosarc (ectoplasm) (PS′), but when it reaches a certain size the endosarc (endoplasm) quite suddenly rushes into it, and the body then begins to flow after the pseudopod. When it is retracted, it is retracted as a whole, there is no flowing inwards first of the endoplasm and then of the ectoplasm.

The movements of the protoplasm and the formation of the pseudopodia go on when all externally is apparently quiescent, and when no definite stimulus is applied to the organism. Obviously there is some inherent response to some sort of stimuli, originating either within or without, manifested by this ceaseless movement; it is similar in its physiological significance to the automatic movements of the higher forms of life, movements which cannot be explained as the immediate response to external stimuli. Thus *Amœba*, the simplest form of life, exhibits **automatism** or **spontaneous movement**. But if it be stimulated by the application of external stimuli, such as being touched by a foreign body, or by the application of a chemical substance, such as a weak acid, or by a weak electric current, it will retract its pseudopodia and assume a spherical form. It is thus **irritable** or responsive towards definite external stimuli, just as higher forms with their more or less elaborately organized nervous systems are; and like them it manifests its irritability by **contraction**, i.e. shortening in one direction with a proportionate lengthening in another, just as they do with their muscles.

When it is hungry it seeks for food by creeping about from place to place until it comes into contact with a particle suitable as food. It feeds mainly on diatoms, desmids, and other unicellular vegetable organisms. It ingests its food particle by causing the tip of a pseudopod to divide and flow round it, and when the two parts meet on the other side, the particle becomes engulfed in the protoplasm of the pseudopod. It is gradually carried inwards to the protoplasm of the body, and becomes immersed in a liquid secreted by the protoplasm, and undergoes gradual disintegration; its soluble portions are absorbed by the protoplasm and built up into its living substance, and the insoluble portion is ejected from some part of the surface of the body. Thus we may distinguish between **vacuoles of ingestion, digestion**, and **egestion**.

Like the higher organisms, *Amœba* thus digests food material, then assimilates it (builds it up into its living substance) and ejects the insoluble residue. It exhibits, therefore, the phenomena of **digestion** and **assimilation**, just as do higher forms of life.

Arising at some part of the endoplasm, its position not being constant, but always near the surface, is a **contractile vacuole**. It gradually dilates (diastole) and then suddenly contracts (systole), at the moment of which radiating canals pass from it to the exterior. Then it begins to form again, dilates and contracts, and so on, as long as the organism lives. Observation has shown that the contractile vacuole contains some nitrogenous body probably allied to guanin ($C_5H_5N_5O$), and it therefore plays the part of an organ of **excretion**, that is, of an organ which gets rid of waste material resulting from the destructive oxidation of the protoplasm.

Oxidation of the protoplasm results, however, not only in the formation of nitrogenous substances of simpler nature, but also of CO_2, derived from the oxidation of the carbon of the protoplasm. And **respiration** consists in the taking in of oxygen, in order that this oxidation may go on ; unless it be taken in, oxidation is not possible, and CO_2 could not be formed. Any evidence therefore that shows that CO_2 is formed by *Amœbæ* is proof that respiration is taking place. If *Amœbæ* be placed in water which has been deprived of its CO_2, and which is kept in an atmosphere devoid of that gas, it is obvious that if after an interval CO_2 is present, it can only have come as the result of the living activity of the *Amœbæ*. If, after some time, to such water there be added baryta-water or lime-water, a milkiness, more or less opaque, is produced, due to the formation of carbonate of barium or calcium, according to the reagent added. The formation of the carbonate from the hydrate shows the presence of CO_2 in the water in which the organisms are living. Moreover, it has been shown experimentally that if *Amœbæ* are placed in water devoid of oxygen, and not in contact with an atmosphere containing it, that their activities cease and they die. Oxygen is therefore necessary for their existence. Like other living organisms, therefore, *Amœba* respires, that is, takes in oxygen and gives out CO_2.

Reviewing the activities of *Amœba*, it is seen to be capable of the performance of all those manifested by the higher and more complex forms. It is irritable and automatic, but it possesses no nervous system ; it is contractile, but it has no muscle ; it is locomotor, but it has no limbs or special organs of any kind for locomotion ; it

can ingest, but it has no mouth; digest, but it has no stomach; excretes, but without excretory organs; and it can respire, but it has no lungs or gills or organs of respiration of any kind. Thus this simple mass of protoplasm, a mere speck of a colloidal substance, can exhibit all the fundamental manifestations of life. The complexity of organization of the higher forms is advantageous to them in the performance of their own special activities, but it is not necessary for the manifestation of life.

The activities just considered pertain to the individual alone, and are necessary for its existence and growth. But were there no others, *Amœbæ* as a race would disappear, indeed would never have appeared. These activities are protective of the individual, but they do not affect the race other than through the maintenance of the individual. And if *Amœbæ* are to be spread in time and space, there must be some means by which they can increase in numbers, or be reproduced. The act of reproduction is in no wise necessary for the existence of the individual, for so long as assimilation and respiration are maintained, the individual will live. Hence, reproduction is an activity protective of the race alone.

Like all its other activities, that of reproduction in *Amœba* is expressed in the simplest form, for as soon as an individual attains the limits of its size, it divides into two portions (Fig. 86, left hand), each of which becomes, by subsequent growth, a new individual. The division of the cell is preceded by that of the nucleus, by karyokinesis (post, p. 351), each half of which retreats to either end; the cell then elongates, then its middle becomes constricted (Fig. 86), and finally the two parts separate.

In *Amœba* the act of reproduction destroys the individuality of the parent, for as an individual it no longer exists, but as two. And as soon as each of these have attained the size of their species they will lose their individuality in the production of their progeny. This is apparently a very different thing to reproduction in higher forms, where the parent, retaining its individuality after its offspring is begotten, ultimately dies. With *Amœba* there is no such thing as death in the natural order of things; it is immortal, because the whole of its substance is merged in its offspring. In higher forms the offspring arises as a mere bud of the parent, which needs the stimulus of the entrance of a bud from another parent before it will develop into an organism. In the immortal *Amœba* there is no sexuality, for mortality is the price of that. Or as Professor Arthur Thomson

poetically expresses it, 'The higher forms have bartered immortality for love.'

It is doubtful if *Amœba* can go on indefinitely reproducing by **simple fission**; for our knowledge of other Protozoa leads us to believe that such a process would ultimately lead to the production of dwarfed forms, and thence to extinction of the race. In the other Protozoa alluded to, this is prevented by a process of conjugation such as that described in *Paramœcium.* And indeed a process of conjugation has been observed in *Amœba*, but its details are not known.

Simple as is the structure of *Amœba*, even simpler forms are to be found. They are amœba-like, but are devoid of a nucleus, and are named *Proto-amœbæ.* It is possible, however, that they may contain the chromatin elements of their nucleus, diffused through the protoplasm in the form of minute granules, or they may even be *Amœbæ* that have lost their nuclei.

CHAPTER XX

EMBRYOLOGY

ALL organisms owe their origin to a pre-existing one, from which there is budded off a unicellular bud or germ, and which by a series of developmental changes, that it is the province of embryology to study, becomes converted into the adult organism. The cyclical development of living things—the origin from the egg, the passage through complicated but definite changes to maturity, to the production of offspring and subsequent death—is one of the distinguishing features of animate things, by which they stand in marked contrast to those of the inanimate world. This fact is expressed in Harvey's aphorism, 'Omne vivum ex ovo.'

After fertilization, and in parthenogenetic animals without fertilization, the egg undergoes the process of **segmentation**, in which it divides repeatedly into segments, which arrange themselves in a definite manner, and ultimately give rise, either to a ball of cells, called a **blastosphere** or **blastula** (Fig. 87), or to a cellular membrane spread out over a limited portion of the surface of the egg, and called a **blastoderm** (Fig. 88). These two early forms of embryo are fundamentally the same, and represent the same stage in the life-history; such differences as they exhibit are related to their form, and depend in the main upon

the size of the egg and the quantity of food material contained in it: in a large egg with much vitellus the early embryo is a blastoderm, and in a small one, with not a great amount of vitellus, it is a blastosphere.

The blastosphere next becomes a sac-like organism, at first consisting of two layers of cells and later of three. This stage is the **gastrula stage** and the sac-like organism is the **gastrula** (Fig. 87). The outer layer of the sac is the **epiblast**, the middle one the **mesoblast** (M), and the inner one, which lines the cavity, the **hypoblast** (H). The cavity itself is called the **archenteron** (M.S), and the aperture through which it communicates with the exterior, the **blastopore** (BP). In a similar way the blastoderm, at first composed of only a single layer of cells, ultimately consists of the same three layers (Fig. 89, E, M, H). With the exception of the lowest Metazoa, i.e. *Hydra*, anemones, corals, and Medusæ, all multicellular organisms pass through this three-layer stage: the three layers are in fact the foundations of the adult, for from them all the organs of which it will consist are derived. Hence they are called the **germinal layers**, and from them the adult organs are derived as follows: from the epiblast, the skin, nervous system, sense organs, and in certain cases the renal organs; from the hypoblast, the epithelial layer of the mid-gut portion of the alimentary canal, together with that of the glands opening into it, such as lungs, liver, and pancreas; from the mesoblast, the organs of circulation, the endoskeleton, the muscular system, the organs of reproduction, and in the majority of instances the renal organs.

It often happens that in the course of its development an organism develops organs which it later loses, and which were of some temporary use to it during its larval existence; other organisms develop organs which at no period of their lives are ever functionally active or are of any use to them: and quite a large number of organisms pass through two or more definitely different stages in their development, in which the earlier stage bears no resemblance to the later, and in which the embryo is a free-swimming and independent form; we then speak of the early embryo as the **larva**, and of the early stage as the **larval stage**. Larval stages are passed through in the development of every organism which arises from an egg that is devoid of or contains but a small quantity of food material, while those which arise from a food-stored egg reach their full development before they are hatched.

The Zoœa larva of the crab and of other Crustaceans possesses

certain spinous processes which are useful as organs of locomotion and to a greater extent for purposes of defence, but which are lost at the termination of the larval stage. Such structures are merely temporary and adaptive, and afford no information as to the genetic affinities of the organism possessing them; they are inconstant and variable, and are differently situated and of different size and form in different Zoæa larva. But there are other characters, such as a large cephalo-thoracic shield, well-developed caudal segments without appendages, a usually forked tail, the six posterior thoracic segments rudimentary, and in front of these seven pairs of appendages, which are constant and appear in all Zoæa; such characters are of importance, since they indicate the probable lines along which the organism to which it will give rise has evolved. We speak of these constant characters as **palingenetic**, and of the inconstant and adaptive ones as **cenogenetic**.

All terrestrial Vertebrata, in the course of their development, possess gill-clefts and blood-vessels in relation to them (Fig. 91); these gill-clefts are never functional, for they never develop gill-filaments, and the clefts play no part in the economy of the organism, and later disappear; while the blood-vessels related to them, and the cartilaginous branchial arches supporting them, become metamorphosed into adult structures. It is impossible to conceive of any intelligent explanation of the temporary presence of typically aquatic organs in wholly terrestrial animals, other than that they are the vestiges of an aquatic ancestor. And similarly with regard to the origin of the hyoid bone and laryngeal apparatus of all terrestrial Vertebrata—man included—from typical fish-like branchial arches.

Considerations of this sort have led to the formation of the modern '**Recapitulation Theory**,' by which it is asserted that every organism in the course of its development passes through structural stages, which represent the stages passed through in the evolution of the race. In other words, the evolution of the individual is a recapitulation of the evolution of the race; or, Ontogeny is summarized Phylogeny. In many instances, however, there is some reason for believing that certain similar features in the development of organisms widely separated may be due to the action of similar environmental factors. But when all allowances have been made for this, there still remains a mass of fact which cannot otherwise be explained other than in terms of the Recapitulation Theory. Such, for instance, are the gill-clefts and branchial arches above mentioned, and in addition there are other

facts, such as that not only the heart, but the whole blood-system of all embryonic terrestrial Vertebrates at a certain stage in their development is fundamentally the same as that of fishes. All Vertebrates, from *Amphioxus* upwards, possess at a certain period in their development an internal rod-like skeleton, called the **notochord** ; in *Amphioxus* and the lampreys this persists throughout life without alteration or addition, but in the higher Vertebrata, from fishes upwards, it is more or less completely replaced, in more primitive forms by a cartilaginous, and in higher forms by a bony vertebral column (post, p. 329). The skeleton of *Amphioxus* is represented by membrane only, if we except the notochord ; that of certain fishes is wholly cartilaginous ; that of Amphibia, partly cartilaginous, partly bony ; while that of birds and mammals is entirely bony. But the cartilaginous skeleton of the above-mentioned fishes, of which the dogfish is one, passes through a membranous stage, and that of the Amphibia, Reptilia, Aves, and Mammalia through both membranous and cartilaginous stages, before it attains its semi-bony or wholly bony condition. In all Vertebrata the nervous system in its early stage is alike and arises in the same way ; but beyond this stage specialization of this or that part occurs. The lungs of the Dipnoans (lung-fishes) arise in just the same way as those of terrestrial Vertebrates, and the complex lung of mammals passes through the simple stage of that of Dipnoans and Amphibia. In all, the alimentary canal and its appended glands arise in fundamentally the same way, and the complex arrangement of that of the higher forms arises only by the specialization of the simpler condition of the lower. To restrict our considerations to animals more similar than a mammal and a fish, let us consider two mammals. The human liver is marked upon its under surface with certain furrows, which in the embryo are more pronounced and deeper, and also more numerous ; comparison of the embryonic liver with that of certain apes shows that the furrows in the former occupy the position of definite fissures in the latter. It has been shown that the fissuring of the liver is probably correlated with its adjustment to the movements of the body, which will be different in animals that adopt the horizontal than in those that have assumed the erect position. Hence the furrows of the human liver are to be regarded as the last traces of fissures present in the liver of an ancestral stock that were more or less horizontal or semi-vertical in their bodily attitudes. In other words, the furrows of the human liver, deeper in the embryo than in the adult, are the expression of one fact in the recapitulation of the race.

Segmentation of the Egg and the Formation of the Gastrula and Blastoderm.

The division or segmentation of an egg may be complete or **holoblastic**, that is, the whole of the egg is divided into segments (Figs. 87 & 90); or it may be **meroblastic** or incomplete, only a limited portion of the egg undergoing segmentation (Fig. 89). The holoblastic segmentation may be **equal** (Fig. 90) or **unequal** (Fig. 87); in the former instance the first formed segments are equal in size, while in the latter the lower segments are larger than the upper.

Some eggs contain no yolk-granules (food granules), or but a very small quantity, and then evenly distributed through the protoplasm of the egg; these are called **alecithal eggs**, and belong to animals which can early obtain their own food by resorting to a larval stage (*Amphioxus*), or to those whose young are nourished by the parent until development is completed (rabbit). In other eggs, named **telolecithal eggs**, there is more or less abundant vitellin (yolk-granules) present; in such the nutritive yolk (vitellin) may be confined more or less to one pole of the egg, while the formative portion at the other pole contains no vitellin, or very much less; the former is the **vegetative** and the latter the **animal** pole of the egg. In telolecithal eggs the germinal vesicle or female pro-nucleus of the egg is confined to the clear protoplasm of the animal pole. The segmentation of this type of egg may be holoblastic if the food material is not very abundant, and meroblastic if it is. **Centrolecithal eggs** are those in which the vitellin is abundant and is confined to a region between an outermost investing layer of formative protoplasm and a central mass of the same material; their segmentation is holoblastic if the nutritive portion of the egg contains a little formative protoplasm, and meroblastic if this portion is wholly composed of vitellin. The egg of the crayfish is a typical meroblastic centrolecithal one.

The Frog's egg (Fig. 87). It is **telolecithal, unequal-holoblastic.** The animal pole is black-pigmented and the vegetative white. The first segmentation is in a vertical plane (1st C), dividing the egg into two equal segments, which are said to correspond to the right and left halves of the body of the embryo. The second segmentation is also vertical, but at right angles to the first; it divides the egg into four similar and equal portions, called blastomeres. In the figure it is not represented since it lies in the plane of the paper. The third segmentation plane (3rd C) is horizontal, but it lies much

nearer to the animal than to the vegetative pole, and therefore divides each of the four blastomeres unequally, into a smaller, upper cell, and a larger, lower one. The two next segmentation planes arise simultaneously; they are vertical and at right angles to each other, and

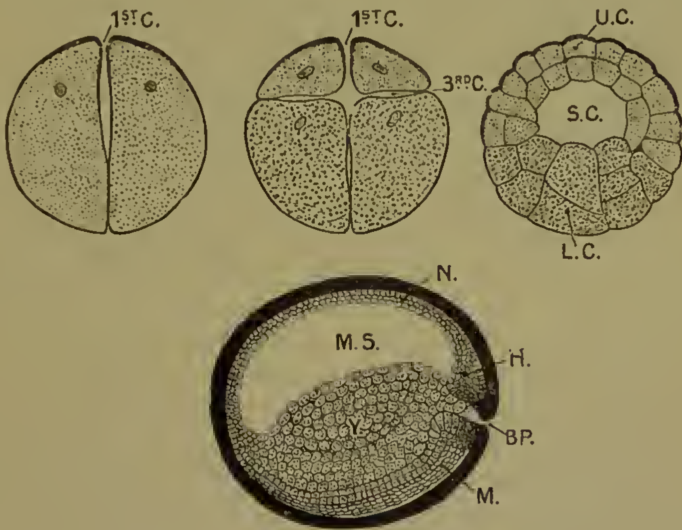


FIG. 87. The segmentation of the egg and formation of the blastula and gastrula of the Frog (*Rana*). From Milne Marshall's *Vertebrate Embryology*. The blastula is the top figure in the right-hand corner, and the gastrula is the lower figure. All the figures represent median vertical sections. 1st C = first segmentation cleft; 3rd C = third segmentation cleft. The second segmentation cleft lies in the plane of the paper, and cannot therefore be represented. BP = blastopore; H = hypoblast; L.C = lower yolk-laden cells; M = mesoblast; M.S = mesenteron; N = notochord; S.C = segmentation cavity; U.C = upper cells (which later become the epiblast). In the gastrula, the epiblast consists of several layers of very small cells, and it is represented by the thick black boundary line.

about 45° to the first two planes. The embryo now consists of sixteen smaller pigmented cells in the animal hemisphere, and an equal number of much larger unpigmented ones in the vegetative. From this stage onwards the segmentation follows no definite rule, the cells dividing independently. The upper cells (U.C) always divide more rapidly than the lower (L.C.), since they are not hindered by the presence of such a large quantity of inert yolk-granules, and consequently remain throughout of smaller size. At about the time when the third segmentation is completed, a small cavity is formed in the interior of the mass of cells at the common junction of them all; this is the **segmentation cavity** or **blastocœle** (S.C). With every subsequent division up to a given stage, the blastocœle increases in size; it is filled with a liquid, and from the first lies nearer the animal than the vegetative pole. The cells are arranged around this cavity, and the

embryo assumes a more or less spherical form; at this stage it is spoken of as a **blastula.** The upper pigmented cells divide rapidly and grow downwards, extending over the lower cells, until all that can be seen of the latter in an external view of the blastula is a small white, circular patch at the vegetative pole. At the outer limit of a part of this white patch there appears a semicircular split, which gradually extends inwards through the mass of large white cells until it opens into the segmentation cavity. At this stage the blastula consists of an outer, upper layer of pigmented cells, called the **epiblast**, of an internal mass of large white cells, which are uncovered by the epiblast at the vegetative pole, and may be called the **yolk-cells**; and between the semicircular split and the epiblast a few layers of small, unpigmented cells derived from the yolk-cells, and constituting the **hypoblast.** The semicircular split gradually extends at the sides and becomes circular; it is now called the **blastopore** (BP), and the mass of white cells confined within its limits, the **yolk-plug** (Y). The hypoblast (H) gradually extends and encroaches upon the blastocœle, which it ultimately obliterates; but at the same time another cavity is formed between the hypoblast and the yolk-cells, which later becomes the lumen of the mid-gut, and is called the **enteron,** or sometimes the **mesenteron** (M.S). The embryo is now oval in form, the enteron communicates with the exterior through the blastopore, the blastocœle or segmentation cavity has disappeared, and there are two definite layers, the epiblast and hypoblast: the embryo is now called a **gastrula** (Fig. 87, lower illustration), and essentially it is of the nature of a double-layered sac, with one portion of the inner wall (that composed of the yolk-cells) much thicker than the other (that formed by the hypoblast). At about this stage the outer layers of the yolk-cells in contact with the epiblast become differentiated and split off from the inner layers, and constitute the third germinal layer or **mesoblast** (M). **At the lip of the blastopore all three germinal layers are indistinguishably fused together.** The lips of the blastopore ultimately come together in the median plane and fuse by concretion. The line of fusion is indicated for some time by a ridge, which is called the **primitive streak,** and there runs along it a slight depression, the **primitive groove.**

The Hen's egg. It is **telolecithal** and **meroblastic.** The ovum is the yolk, and the white of egg and shell are accessory parts added to it while passing down the oviduct. At the period when it is just liberated from the ovary and enters the funnel-like expansion of

the upper extremity of the oviduct, it is a large, yellow, globular body, invested in a vitelline membrane. Its formative protoplasm is very small in quantity and is confined to the animal pole, while the nutritive protoplasm constitutes practically the whole mass of the ovum; the nutritive portion consists of spherules of food-yolk (Fig. 89, Y), which are of two kinds: yellow-yolk spherules and white-yolk spherules. The latter are confined to a central mass and to a column passing from the centre upwards to the animal pole, whence it spreads as an exceedingly thin layer over the surface of the ovum, beneath the vitelline membrane (Fig. 96, V); the former are arranged in concentric layers round the central mass (Fig. 96, right-hand figure), and separated from each other by thin layers of white-yolk.

Impregnation takes place while the egg is in this condition and in the upper part of the oviduct.

While passing down the oviduct, the ovum becomes surrounded by many layers of albumen, alternately denser and less dense, secreted by the wall of the genital duct; farther down it is invested by the shell-membranes and the shell. At either extremity of the equator of the ovum there is developed a coiled mass of dense albumen, called the **chalaza**; they probably function as 'buffers,' tending to protect the yolk from mechanical injury. At the broader end of the egg the shell-membrane is separated from the shell, leaving a space called the air-chamber, and with which later the allantois comes into partial relation.

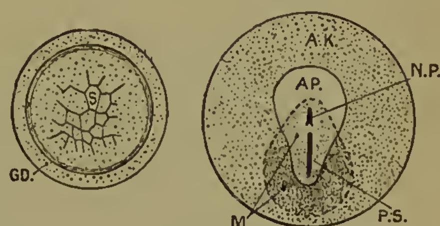


FIG. 88. The left-hand figure represents a surface view of an early stage in the segmentation of the germinal disc of the chick's egg; the right-hand one a diagrammatic representation of the blastoderm of the hen's egg at about the twentieth hour of incubation. (From Marshall's *Vertebrate Embryology*, after Coote and Duval.) AP=area pellucida; AK=area opaca; GD=germinal disc; M=mesoblast (its limits at this stage are shown by the dotted line); N.P=neural plate; P.S=primitive streak.

Segmentation commences in the lower part of the oviduct before the egg is laid; it is meroblastic, being confined to the **germinal disc** (Fig. 88, GD). This latter is composed of the patch of formative protoplasm at the animal pole that contains the **germinal vesicle**. The segmentation is characterized by its constant symmetry, and by the fact that the earlier divisions do not extend through the full depth of the germinal disc. The first segmentation groove is vertical, and extends nearly across the width of the germinal disc (Fig. 88, GD).

This is followed by a second, which is almost at right angles to the first one. Four other furrows, radial in direction, at right angles to each other, and disposed at about 45° to the two first formed ones, then appear. Each of the eight blastomeres (S) thus formed is then divided, by a vertical cross furrow, into an inner smaller and an outer larger cell; the whole is thus divided into a central portion of eight small cells, and a peripheral portion of eight much larger cells. From the first the furrows are excentric, extending nearer to the margin of one side of the disc than to the other; the segments are smaller on the side of the disc over which the furrows have the farther extended, and bigger at the other (Fig. 88). The posterior end of the embryo corresponds to the side of the smaller segments, and the anterior to the other. Other furrows now rapidly appear and cut up the germinal disc into a number of cells of irregular form and size, all of which are arranged in a single layer and still attached to the yolk, i.e. the furrows are all vertical. A little later, horizontal clefts appear, cutting off the cells of the central part of the disc from the deeper part beneath, but not yet affecting the outer cells. Vertical and horizontal clefts then appear in the deeper portion of the disc, and give rise to two layers of cells. The germinal disc has now become converted into a patch of cells, consisting of an outermost layer, the **epiblast** (Fig. 89, A, E), and of deeper, larger cells, lying between the epiblast and the yolk; this membranous structure is now called the **blastoderm.** Between the lower layer cells and the epiblast there is a chink or space, which may be called the **segmentation cavity**, since it probably corresponds to that of the frog's blastula.

Examination of the surface of the blastoderm will show that at this period (just preceding the act of laying) it is a small circular patch, about 3–4 mm. in diameter, on the surface of the yolk; its margins (Fig. 88) are more opaque than its central part, hence its division into an **area pellucida** and an **area opaca.** The blastoderm now slightly extends over the surface of the egg, and the lower layer cells become divided up into a larger number of smaller ones with rounded form.

At about this stage the egg is laid and incubation begins. The blastoderm rapidly extends, and at about the end of the second or third day covers nearly one-half of the surface of the egg. In the course of this extension the area opaca (Fig. 88, AK) remains circular, but the area pellucida (AP) becomes elongated and broader at one end than the other; the broad end corresponds to the head end

of the embryo. Two or three hours after incubation has commenced the lower layer cells become flattened and merge together, and form a continuous membrane; this is the **hypoblast** (Fig. 89, A, H). A few of the lower layer cells remain between it and the epiblast, and in part later contribute to the formation of the mesoblast (M).

During the course of the changes above mentioned, the lower layer cells, which at first were continuous with the epiblast round its margins, become separated from that except at its posterior end, where they still remain fused. This fused patch gives rise to a

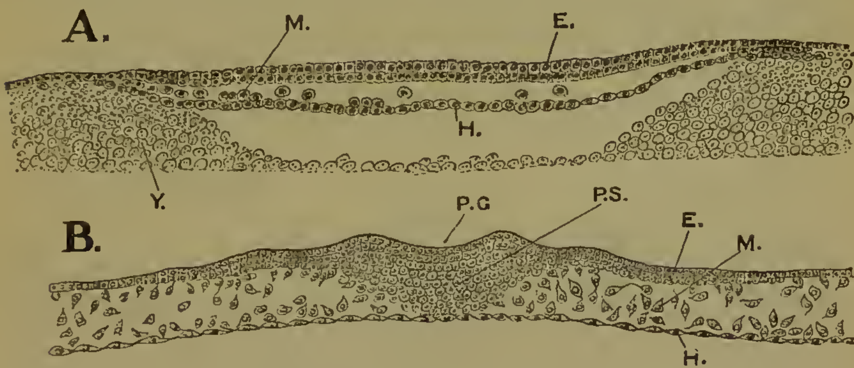


FIG. 89. A. Transverse section through the blastoderm of a chick at the thirteenth hour of incubation. B. A similar section through the region of the primitive streak at the nineteenth hour. E = epihlast; H = hypoblast; M = mesoblast; P.G = primitive groove; P.S = primitive streak; Y = yolk-spherules.

crescentic opacity when the blastoderm is viewed in surface view; in the earlier hours of incubation it becomes drawn out into a streak, extending from the margin to near the centre of the blastoderm, when it is known as the **primitive streak** (Fig. 88, P.S); it is traversed along its whole length by a shallow groove, the **primitive groove** (Fig. 89, B, P.G). Examination of transverse sections of the blastoderm (Fig. 89, B), passing through the primitive streak, shows that the latter arises by proliferation of the cells of the epiblast in the median line on the under surface. At this point the hypoblast is confluent with the primitive streak.

Between the twelfth and twentieth hour of incubation the **mesoblast** arises (Fig. 89, A, M) partly from the lower layer cells that were not concerned in the formation of the hypoblast, partly from cells derived by proliferation of the margin of the hypoblast, and partly by extension of the lateral edges of the deeper cells of the primitive streak. The three masses of cells formed from these three sources

soon become confluent and form a continuous sheet of mesoblast (Fig. 88, M), widest on either side of and behind the primitive streak, but narrowing rapidly in front of that.

The primitive streak probably represents the coalesced lips of the blastopore, and the primitive groove the line occupied by the obliterated aperture. This theory of the nature of the primitive streak is called the '**Concrescence Theory**,' and the student will do well to turn back to the description of the formation of the streak in the gastrula of the frog (p. 310), and to note that at the lip of the blastopore in the frog, as at the primitive streak in the chick, the mesoblast, hypoblast, and epiblast are confluent.

The Rabbit's Ovum. The egg is **alecithal** and segmentation **equal-holoblastic** (Fig. 90, A). When discharged from the ovary

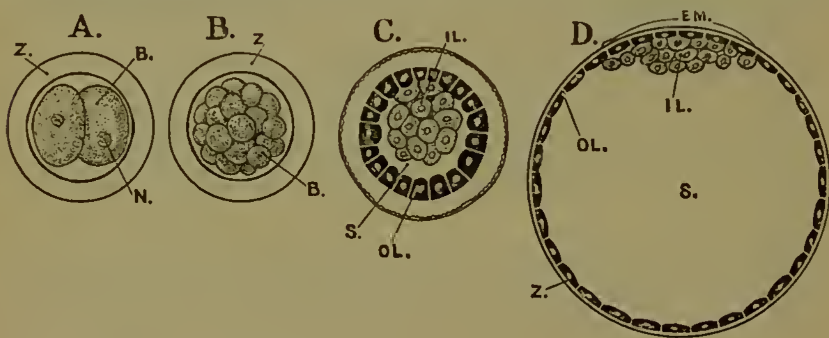


FIG. 90. Segmentation of the Rabbit's ovum. A. An ovum twenty hours after copulation. B. An ovum at the middle of the third day, and showing the morula stage, just before completion of segmentation. C. An ovum seventy-five hours after copulation, in optical section, and showing the first formation of the blastodermic vesicle. D. Section of the blastodermic vesicle at the end of the fourth day. A and B from Marshall's *Vertebrate Embryology*, after Bischoff; C and D from the same source after Van Beneden. B = blastomere; EM = embryonal area; IL = inner layer of cells; OL = outer layer of cells; N = nucleus; S = segmentation cavity; Z = zona radiata. The thin line outside the zona radiata represents the vitelline membrane.

it is invested in a vitelline membrane and a zona radiata (Z). Fertilization occurs in the upper part of the Fallopian tube, whence the egg travels down until it reaches the uterus. Segmentation commences about 10–12 hours after fertilization is effected, and is continued for the following two days.

The first division divides the egg into two nearly equal ovoid cells (Fig. 90, A, B); the difference between the size of the two cells is barely perceptible. The next division cuts each of these two cells into two; each of the four thus produced divide again, making eight altogether. The four cells derived from the smaller of the first two

form a kind of shallow cup lying upon and partially enclosing the four larger cells derived from the larger of the first two. The upper smaller cells now divide more rapidly than the larger ones, and more completely enclose them (Fig. 90, B); and at about the seventieth hour after fertilization the large cells are so completely enclosed that only a small portion—a little spot—is visible in a surface view. This small aperture in the outer cells has been called the blastopore by some investigators.

At about this stage the segmented egg enters the uterus; and very shortly afterwards the **outer cells** (Fig. 90, C, OL) have grown round and completely enclose the larger **inner ones** (IL). Owing to the rapid growth of the outer cells, the inner ones become separated from them, except at one spot (Fig. 90, C); the cavity thus formed between the inner and outer cells becomes filled with fluid. The cellular ball at this stage is called a **blastodermic vesicle**; and in the main it probably corresponds to the blastula or early gastrula stage of *Amphioxus* and the frog. The vesicle grows very rapidly, and by the end of the fourth day it is about 0·3 mm. in diameter, and consists of an outer wall of small, somewhat flattened cells, with a lenticular mass of larger rounded cells attached at one point within (Fig. 90, D). The cavity of the vesicle (S) (=? segmentation cavity) is now very large. The mass of inner cells now begins to spread out over the inner surface of the vesicle and to lose its lenticular form; at its margin it is but a single layer of cells thick, but two or three at its centre. The vesicle next elongates and becomes ellipsoidal.

The exact nature of the changes which next follow is a little doubtful, since observers do not agree, and further investigation is much needed. We shall give one account. The surface at which the inner cells are attached to the wall of the vesicle and which is indicated in surface view by an oval patch, is called the **embryonal area** (Fig. 90, EM). The inner cells next divide into two layers: an upper one of cubical cells and a lower one of flattened cells; the latter extends beyond the former round its margins and comes into contact with the wall of the vesicle. It is then stated that in the embryonal area, the outer layer of cells (wall of the vesicle), here called **Rauber's layer**, disappears; how it disappears is not known, and perhaps it may become confluent with the upper of the two layers derived from the inner cells. Whether that be so or not, the upper of these two layers, which now forms the surface of the vesicle in the embryonal area, is called the **epiblast**; at its margins it is continuous

with the wall of the vesicle (OL), which is now also called epiblast. The cells of the epiblast of the embryonal area are columnar, while those of the remaining portion are flattened. The lower layer of cells is called the **hypoblast** ; it extends beyond the limits of the embryonal area and lines about a third of the vesicle.

Towards the end of the seventh day the epiblast thickens on its under surface, in the median line, by proliferation of the cells along this tract of the layer; this thickening forms the **primitive streak**, and along its upper surface the **primitive groove** soon appears. By lateral extension of the wings of the primitive streak, between the hypoblast and epiblast, the **mesoblast** is formed. The primitive streak, and in part the mesoblast, thus arise in the same way as in the chick.

Further Development of the Chick.

We have seen that the blastoderm is a three-layered membrane (Fig. 89, A) lying at the animal pole of the ovum, and containing at the posterior end of the area pellucida (Fig. 88, A.P) the primitive streak (P.S). The embryo itself (N.P) arises in front of this streak, its long axis lying parallel to that of the streak; it extends forwards to the anterior end of the area pellucida, at which end its head is situated. As development proceeds the area opaca (A.K) becomes relatively very broad and its inner margin becomes the seat of a very rich formation of blood-vessels, in consequence of which this part of it is distinguished as the **area vasculosa**. Between the second and third day the largest of these blood-vessels have become gathered into two large ones lying on either side of the embryo ; these are the **vitelline veins** (Fig. 91, V.V), and they pass inwards to the embryo, uniting on its ventral surface to form the rudimentary tubular heart (AU, V, & B, H) at about the middle of the second day.

The embryo arises at about the twentieth hour of incubation, and is essentially formed by an upfolding and constricting off of a portion of the area pellucida. At about the thirty-sixth hour the rudiments of the brain, spinal cord (Fig. 96, S., C.V), heart, notochord, body cavity, and mesoblastic somites (Fig. 91, MY) have appeared. The axis of the embryo is straight (Fig. 96, left-hand top figure), and is usually but not invariably disposed at right angles to the long axis of the egg. For the first thirty-six hours the constricting off of the embryo proceeds slowly, and it is mainly the head end that is affected. By the third day the tail end and the sides of the body are clearly defined

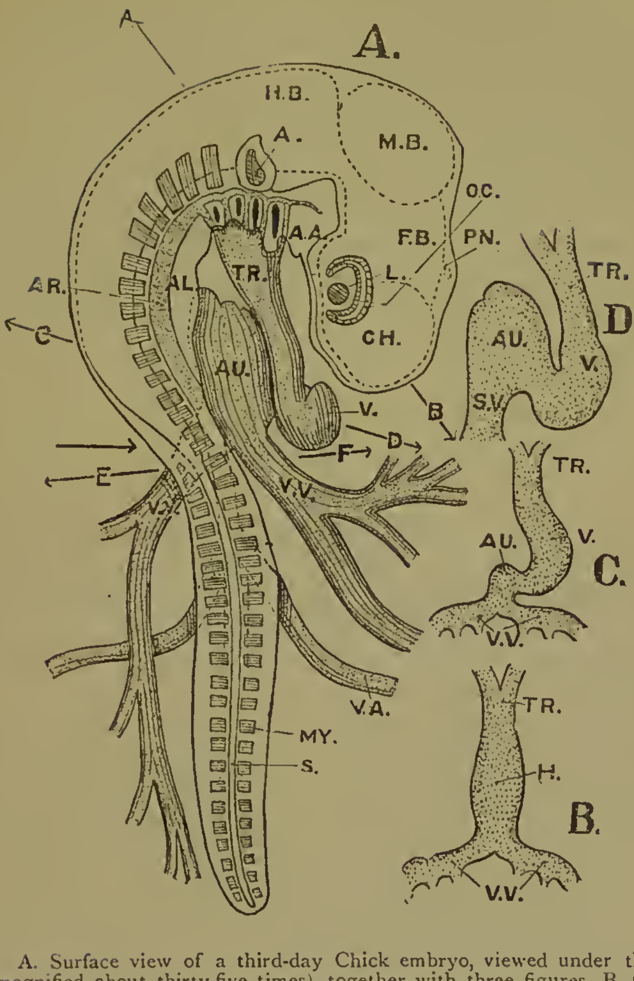


FIG. 91. A. Surface view of a third-day Chick embryo, viewed under the two-thirds objective (magnified about thirty-five times), together with three figures, B, C, D, on the right representing three stages in the development of the heart. At about the third day the anterior end of the embryo twists round through a right angle, the place where the twist occurs being indicated by the unlettered arrow on the left; the embryo thus presents a lateral aspect above the arrow and a dorsal one below. At this stage in development the fourth and fifth aortic arches (A.A) are not present, but have been put in for greater completeness. The embryo has been represented as it would be seen when it had been suitably preserved and rendered transparent. B. The heart at about the middle of the second day. C. The same at the close of the second day. D. The same at the third day. A = auditory pit; AU = atrium; AL = alimentary canal (mesenteron); AR = dorsal aorta; A.A = aortic arches, the gill-clefts are the elongated black tracts between them; CH = cerebral hemispheres; F.B = fore-brain; H = heart; H.B = hind-brain; L = optic lens; M.B = mid-brain; MY = protovertebræ, myotomes, or somites; O.C = optic cup; PN = pineal body; S = spinal cord; S.V. = sinus venosus; TR = truncus arteriosus; V = ventricle of heart; V.A — vitelline artery; VV = vitelline veins. The lines A—B, C—D, E—F, represent planes of sections, the figures of which are represented in FIG. 92. The representation of the Chick embryo is after Duval, slightly altered by having the nervous system indicated by a dotted line.

from the yolk-sac by the constriction that has now extended from the head backwards; at the end of the third day the anterior end of the embryo has turned through a right angle (Fig. 91), so that the head and anterior part of the body lie upon the yolk upon their left side, instead of upon their ventral surface as before. The posterior half of the embryo still retains its original arrangement, i. e. its dorsal surface faces upwards, and its ventral downwards to the yolk-sac. The head is strongly flexed, since the anterior part is bent through a right angle upon the posterior portion: this is called the **cranial flexure** (Fig. 96). By the fourth day the constriction has been carried so far, that the embryo is only attached to the yolk-sac (Fig. 96, Y) (the sac formed by the investing blastoderm and vitelline membrane round the yolk) by a very short stalk which opens into the gut (G).

At about the thirtieth hour a fold of the blastoderm begins to rise up in front of the chick (Fig. 96, AM) and gradually extends right round to the tail; this extends also upwards and over the embryo from all sides, and by the fourth day has completely covered in the whole of the embryo (Fig. 96, right-hand figure). This membranous covering, which as we shall later learn has a double wall, is called the **amnion**; it is characteristic of the embryos of reptiles, birds, and mammals (= **Amniota**), and is absent from those of fishes and Amphibia (= **Anamnia**).

At about the thirty-sixth hour a vascular sac-like outgrowth (Fig. 96, A) of the hinder part of the intestine arises, which grows backwards behind the embryo and then dorsalwards; by the end of the fourth day it has not reached very great dimensions, but by the end of the ninth day it has spread out between the embryo and the egg-shell as a large flattened sac (Fig. 96, left-hand lower figure): it is called the **allantois** or **allantoic sac**. Its function is respiratory, for blood is brought to it by the two allantoic arteries and returned from it to the heart by the allantoic veins, via the vitelline veins.

By the end of the fourth day rudiments of the limbs have appeared.

DEVELOPMENT OF THE ORGANS.

I. The Epiblastic Organs.

The Nervous System. First day. Shortly after the appearance of the notochord, about the twentieth hour, the epiblast above it begins to thicken; this thickened tract is the rudiment of the nervous system and is called the **neural plate** (Fig. 88, N.P). By the end of the

first day it has considerably lengthened, and a groove, the **neural groove**, has formed along the dorsal surface of its whole length by a slight upfolding of its walls, each of which is called a **neural fold** (Fig. 95, A). Posteriorly, the neural folds diverge and embrace the anterior extremity of the primitive streak between them. Anteriorly, by the twenty-fourth hour the neural folds have grown upwards and turned inwards towards the middle line, so that they have now converted the open groove into a closed canal, the **neural canal** (Fig. 95, B, N.C). The part of the groove that first becomes closed corresponds to the future hind-brain of the embryo, and from this point the closure of the groove proceeds rapidly both forwards and backwards. Anteriorly, the blastoderm has become folded downwards and beneath the head part of the embryo, so that that lies lifted above the surface of the blastoderm, and a transverse section taken through this region would show the neural tube cut through above, and the blastoderm, apparently unconnected with it, below.

Second day (up to forty-eighth hour). At the commencement of the second day the neural tube dilates at its posterior end to form the **cerebral vesicle** (Fig. 96, C.V); this becomes divided by two shallow constrictions into three vesicles: the **fore-brain** (F.B), **mid-brain** (M.B), and **hind-brain** (H.B). Of these the mid-brain (Fig. 91, M.B) is the smallest, and the hind-brain the largest (H.B); very shortly after its formation the roof of the latter becomes thin and membranous (Fig. 92, A, H.B). By about the middle of the second day the whole length of the brain, and, a few hours later, the whole length of the neural groove (spinal cord) also, become closed by fusion of the neural folds (Fig. 95). The last part to close is near the summit of the fore-brain, and it is from this point that the pineal outgrowth (Fig. 91, PN) later arises. Between the beginning and middle of the second day the brain becomes bent upon itself, the mid-brain lying at the apex of the bend; this is the **cranial flexure**, and as a result of its formation, the fore-brain is carried round to the ventral surface of the head (Fig. 91).

Fore-brain. The fore-brain is characterized by the number of outgrowths to which it gives origin. From its dorsal wall the **pineal stalk** (Fig. 91, P.N) grows out; from its lateral walls the **optic vesicles** (Fig. 93, A, OC); from its ventral wall the **infundibulum** (Fig. 93, I); and from its anterior wall the **cerebral vesicles** (Fig. 91, C.H). These latter arise, at about the middle of the second day, as a median unpaired outgrowth of the fore-brain, called the **vesicle of the hemi-**

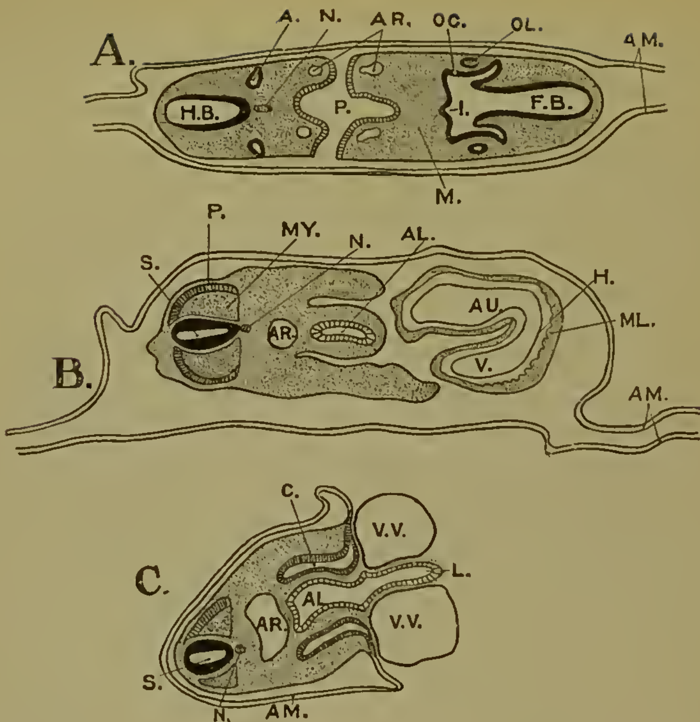


FIG. 92. Three transverse sections taken through three different regions, the plane of which is indicated n Fig. 91. A. Section in the plane A—B. B. Section in the plane C—D. C. Section in the plane E—F. A. & B. 60 hours; C. 50 hours. A=auditory vesicle; AL =alimentary canal (which will become œsophagus in B, and proximal end of intestine in C); AR=aorta; AM=amnion; AU=auricle of heart; C=cœlom or body cavity; F.B= fore-brain; H=hypoblastic layer (endocardium) of heart; H.B=hind-brain; I=infundibulum; L=hepatic diverticulum (origin of liver); M=mesoblast; ML=muscular layer of heart; MY=myotome; N=notochord; OC=optic cup; OL=optic lens; P=pharynx in A, but muscle plate in B; S=spinal canal; V=ventricle of heart; V.V=vitelline veins.

spheres; this later, on the third day, grows forwards as two antcrior horns, which become the **cerebral hemispheres** (C.H). From the anterior extremity of each cerebral hemisphere the **olfactory lobes** arise as hollow buds on about the eighth day. On the second day the infundibulum (Fig. 93, A, I) is only indicated by a deprcssion in the floor of the fore-brain. At the commencement of the second day thc **optic vesicles** (Fig. 93, A, OC), which become the retina of the eycs, arise as a hollow outgrowth from the side wall of either side of the fore-brain.

The **mid-brain** undergoes but little change during the sccond day.

The walls of the **hind-brain** arc at first of nearly equal thickness all round, but at the end of the second day they becomc thickened on

the sides and floor, while the roof becomes much thinner. The hind-brain becomes the **medulla oblongata** of the adult and its cavity the **fourth ventricle.** The **cerebellum** first appears, about the end of the second day, as a transverse thickening of the roof of the hind-brain, immediately behind the constriction dividing that from the mid-brain.

Third day. Fore-brain (Thalamencephalon). At the commencement of the third day the **pineal stalk** arises as a median tubular outgrowth from the thin-walled roof of the thalamencephalon, at about the middle of its length; by the end of the third day it has grown forwards and lies close beneath the outer epiblast. At a later period it dilates at its free extremity to form the **parietal organ**; this latter, however, in the chick, never assumes the structure of an eye. The infundibulum becomes more pronounced, and the floor of the fore-brain in front of it has become thickened, but otherwise there is but little change. The cerebral hemispheres have grown bigger and form a pair of prominent rounded swellings. The further development of the optic vesicles will be studied later. The side walls and floor of the thalamencephalon are more thickened, but the median tract of the roof remains thin.

Mid-brain. This still retains its approximately spherical form and undergoes no important change.

Hind-brain. The roof has now become reduced to a single layer of epithelial cells, and the side walls and floor are thicker than before (Fig. 92, A). The cerebellum is still only a transverse thickening of the roof of the hind-brain.

Fourth day. Thalamencephalon. Other than a continued thinning of its roof and the increase in size of the infundibulum, the thalamencephalon has undergone but little change. It now consists of a chamber with thickened side walls and floor, and a reduced roof. As a down-growth of its thickened floor there is now a well-defined infundibulum, from its roof the tubular pineal body projects, from its lateral walls the optic vesicles, and from its anterior wall the large and well-defined paired cerebral hemispheres.

Mid-brain. Up to the end of the fourth day this has undergone but little change, but early on the fifth a pair of rounded swellings grow out from its roof; these later develop into the **optic lobes.**

Hind-brain (Medulla oblongata). This has undergone but little change. The roof shows signs of becoming folded; later, about the ninth day, these folds are very pronounced and carry blood-vessels in

them. The vascular epithelial membrane becomes the choroid plexus of the adult. The cerebellum is still only a transverse thickening of the roof, but later, at the eighth day, it grows upwards as a transversely disposed outgrowth. It thickens, and its walls become folded, so that in section it exhibits a crescentic-rosette appearance.

The Sense Organs.

The Eye. Second day. As already stated the optic vesicles arise from the side wall of the fore-brain as a pair of hollow outgrowths. These become partially constricted off from the brain, and they then only remain connected with it by a short stalk, the **optic stalk** (Fig. 93, OS). Towards the end of the second day the optic vesicle (OC) is a spherical sac connected with the brain by the hollow optic-stalk; its outer surface is in contact with the outer epiblast. By the end of the second day there is formed in the epiblast, where it is in contact with the vesicle, a circular thickened patch (Fig. 93, A, OL). By the forty-eighth hour (Fig. 93, B) this thickened patch has become pitted in, and is now called the **vesicle of the optic lens** (OL). It presses in upon the optic vesicle, as a result of which that becomes indented, and forms a kind of shallow cup, now called the **optic cup** (Fig. 93, B).

Third and fourth days. The pitting in of the epiblastic vesicle of the optic lens proceeds rapidly, so that in the early part of the third day (Fig. 93, C, OL) it has become a spherical sac with a minute aperture formed by the infolding lips of the indentation. By the middle of the third day the lips meet and become confluent, and the vesicle of the lens becomes completely constricted off from the external epiblast (Fig. 92, A, OL). The inner wall of the vesicle then thickens rapidly, and by the end of the fourth day (Fig. 93, D, OL) it has come in contact with the outer wall, and has completely obliterated the cavity of the vesicle.

Meanwhile the optic cup has been deepening by the inpushing of its inner wall, and by the end of the third day the original cavity of the optic vesicle has become almost obliterated by the opposition of the two walls of the optic cup (Fig. 93, C & D). The margin of the optic cup remains in contact with the border of the lens, except at one point (Fig. 93, B, F), where a small space is left. As the cup and lens grow, this small space elongates out in the form of a fissure, called the **choroidal fissure.** Through this the mesoblast surrounding the cup

grows inwards and fills the space between the lens and the wall of the cup; the intruded mesoblast becomes the vitreous humour. The fibres of the optic nerve also pass out through it on their way to become connected with the brain. Of the two layers of the optic cup the inner is by the third day much the thicker (Fig. 93, C)—it is thicker from the beginning but the difference is now more marked—and it ultimately gives rise to the retina (Fig. 93, D, R), of the histological

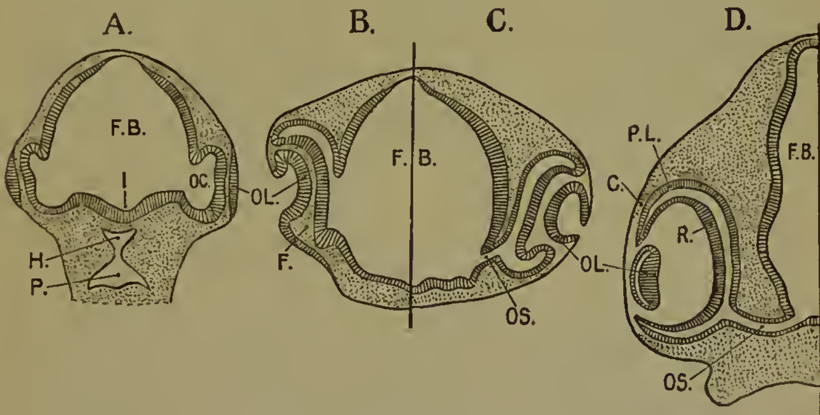


FIG. 93. Four transverse sections in the region of the fore-brain to show the development of the eye. A. 46 hours. B. 48 hours. C. 52 hours. D. 80 hours. C = mesoblast that will form the cornea; F = choroidal fissure; F.B = fore-brain; H = hypophysis; OC = optic vesicle or optic cup according to stage of development; OL = vesicle of optic lens in B, C, and D, but the epiblastic thickening that precedes its formation in A; OS = optic stalk; P = pharynx; P.L = pigment layer of retina; R = sensory layer of retina.

elements of which, that of the rods and cones—the essential light-perceiving element—is the last to be differentiated. The outer layer (P.L) of the cup is by the fourth day reduced to a single layer of flattened cells, which become deeply pigmented, and ultimately form the pigment layer of the retina.

The sclerotic, choroid, and eyelids arise from the mesoblast surrounding the optic cup, as do also the muscles that move the eyeball. The iris arises from that part of the marginal portion of the optic cup which is not converted into retina. The two layers of this part of the cup become confluent and deeply pigmented, and later become connected with the choroid, with which in the adult it becomes continuous. The iris then grows forwards, reducing the aperture in front of the eye to a narrow aperture or pupil. The eyelids are formed by protruding masses of mesoblast growing into outwardly projecting folds of the epiblast.

In all probability the fibres of the optic nerve arise, as in the frog, from the inner layer of the optic cup, and grow inwards along the optic stalk to the brain.

The Ear. The origin of the ear is very similar to that of the optic lens; it arises as a thickening of the epiblast (Figs. 91 & 94, A, A), dorsal to the gill-slits and on either side of the hind-brain (H. B). The thickened patch becomes indented by the middle of the second day to form the **auditory pit**; this, by a process similar to that of the formation of the optic vesicle, becomes constricted off from the external epiblast to form the **auditory vesicle** (Fig. 92, A & Fig. 94, B, A & A′), which gradually sinks deeper into the mesoblast. The auditory vesicle grows larger, and by about the fourth day becomes partially divided into two cavities, a lower and outer **sacculus** and an upper and inner **utriculus** (Fig. 94, C, S), by the formation of a septum which remains permanently perforated in its middle. The semicircular canals arise from the utriculus about the seventh or eighth day. The cochlea arises as an outgrowth of the sacculus at a later period.

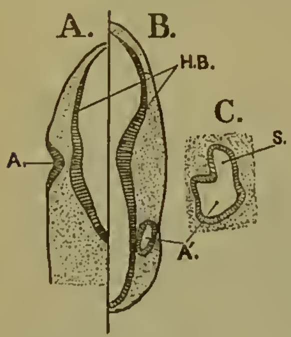


FIG. 94. Two transverse sections through the hind-brain to show the formation of the auditory vesicle. A. 52 hours. B. 60 hours. C. the auditory vesicle at the sixth day. A = auditory pit; A′ = auditory vesicle; H.B = hind-brain; S = utriculus. In C A′ points to the sacculus.

At about the end of the second day the auditory nerve becomes connected with the auditory vesicle upon its antero-inner surface. The nerve arises as a branch of the seventh or facial nerve, and it grows backwards to become connected with the auditory vesicle. As the ampullæ, sacculus, utriculus, and cochlea are developed the nerve splits into branches which by the growth of the ear become carried apart, but retain their connexion with their respective portions. In its mode of development the auditory nerve corresponds to the cutaneous branch of a cranial nerve. The auditory nerve is not, therefore, a special cranial nerve.

The Nose. At the end of the second day a pair of thickened patches of the epiblast appear on the under surface of the anterior part of the head; these later become involuted and form two spherical sacs opening to the exterior. The apertures are at first wide and round, but later become smaller and slit-like; they remain perma-

nently open as the **external nares.** The wall of each olfactory pit becomes thrown into numerous folds and gives rise to the sensory epithclium of the adult nasal organ. The olfactory nerves very early (about the third day) become connected with the olfactory sacs by growing outwards from the brain to the sacs.

The apertures (external nares) do not open into the stomodæum, but immediately in front of that; but at the fourth day a groove appears, which runs from the rim of the narial aperture to the antero-outer angle of the stomodæum. This groove on the fifth day becomes converted into a tube by the coalescence of its lips; it forms the **posterior narial passage.** As the mouth elongates by the formation of the beak a horizontal, plate-like process arises from either maxilla, and, growing inwards, both coalesce in the middle line to form the hard palate: the cavity of the stomodæum is thus divided into an upper respiratory chamber, the **narial chamber,** and a lower nutritive one, the **buccal cavity.** The hard palate extends back into the posterior end of the stomodæum, and at this part the narial chamber opens into the pharynx or most anterior part of the hypoblastic (mesenteron) gut. The posterior narial passage opens into the narial chamber, and the result of the formation of the hard palate is that the communication of the olfactory organ with the buccal cavity is carried farther back and opens into the pharynx.

The Skin. The epidermis and the glands opening upon its surface are developed from the epiblastic layer covering the embryo. Feathers arise from epiblastic papillæ, the bases of which sink deeply into the epiblast: from the apices of these papillæ the primitive or **down-feathers** are developed, and later, the **permanent feathers** arise in essentially the same manner from the bases. The epiblastic papillæ do not arise until about the eighth day of incubation.

The Stomodæum. This arises on the second day as a shallow pit-like depression of the epiblast near the base of the head-fold. From the first it is separated from the anterior end of the mesenteron (=pharynx) only by a thin layer of mesoblast. On the third day the floor of the stomodæum thins and the pit becomes slightly deeper; at the end of the day the floor becomes absorbed, and the stomodæum is in open communication with the pharynx. From its dorsal wall, at the end of thc second day, a small diverticulum ariscs, which becomes related to the infundibulum and the anterior extremity of the noto-chord. By the cnd of thc third day this diverticulum assumes the form of a tube, blind at one end, and at the othcr opening into the

buccal cavity (stomodæum). At its blind end, on the eighth day, it gives off a number of branching tubular processes which become highly vascular. On the twelfth day it loses its connexion with the buccal cavity by obliteration of the cavity of its tube. This organ is the **pituitary body** and is of unknown significance or function. The stomodæum becomes the buccal cavity of the adult.

The Proctodæum. This arises as a very shallow pit in the epiblast, just in front of the extremity of the tail and near the posterior termination of the mesenteron. At the fifteenth day it acquires an opening into the gut. The cloaca of the adult bird consists of three chambers : an anterior, median, and posterior one, and of these the proctodæum gives rise to the posterior one alone.

II. The Hypoblastic Organs.

Notochord. At the twentieth to twenty-fourth hour of incubation, the hypoblast cells along the median line of the layer and in front of the primitive streak become more densely aggregated than elsewhere in the layer. About the twenty-fourth hour this rod of densely packed cells separates from the hypoblast and comes to lie between it and the epiblast above and the mesoblast on either side (Figs. 95 & 96, N). This rod is the primitive endoskeleton, and is formed early in the development of all Vertebrates ; it is called the **notochord** (N). Its posterior extremity is continuous with the anterior end of the primitive streak, and, inasmuch as that is continuous with epiblast and mesoblast, it follows that at this point all three layers, epi-, meso- and hypoblast, are continuous ; this continuity is extended backwards along the whole length of the primitive streak. The only point in the gastrula of the frog where the three germinal layers are thus continuous is at the lip of the blastopore, which as it closed became extended in the form of a streak, and later, at this point, the posterior end of the notochord fused with all three layers ; the primitive streak—at any rate the anterior part—of the chick is thus probably homologous with the blastopore of the frog.

The Alimentary Canal. The alimentary canal arises from three portions, of which one is hypoblastic and the other two epiblastic in their origin. The **buccal cavity** and the posterior portion of the **cloaca** arise respectively from the stomodæal and proctodæal invaginations of the epiblast, and the formation of which has already been described. The greater length of the alimentary canal, i.e. the

pharynx, the temporary **gill-slits**, **crop**, **œsophagus**, **gizzard**, **duodenum**, **jejunum**, **ileum**, **rectum**, and anterior portion of **cloaca**, as well as the epithelial lining of the glands (liver and pancreas) and their ducts opening into it, arise from the hypoblast. This hypoblastic portion of the alimentary canal is called the **mesenteron**, and it arises by the infolding of the hypoblast and splanchnopleuric layer of the mesoblast (Fig. 95, H & M), until the lips of the folds meet and fuse. There is thus formed a straight tube, closed at all parts except one where the mesenteron communicates by a wide and short tube with the yolk-sac (Fig. 96, G & Y): the short tube is called the **yolk-stalk**. The mesenteron thus consists of a straight tube, running from the stomodæum backwards to the tail, lined by hypoblast and covered externally by the splanchnopleuric layer of the mesoblast (Fig. 92, B & C, AL). It remains straight up to the end of the fourth day, after which it becomes markedly convoluted.

The anterior portion of the mesenteron gives rise to the **pharynx** (Fig. 92, A, P); it is wide from side to side, and narrow from front to back. Towards the end of the second day the gill-pouches arise as paired evaginations of the hypoblastic lining; they are four in number (Fig. 91, behind A.A), and are developed from before to behind. The evaginations gradually extend outwards, and between the end of the third day and the fifth they meet the external epiblast, and the line of junction becomes perforated to form the **gill-clefts** (Fig. 92, A). In their mode of development, and in their structural relationships, the gill-pouches and gill-clefts of the chick agree with those of fishes and tadpoles; they differ in that they never develop gill-filaments. The parts of the pharyngeal wall between the gill-pouches are called the **visceral arches**, and the first three only of these, in the chick, are supported by skeletal elements. The first of these arches is the **mandibular arch**, and later forms the basis of the lower jaw; the second is the **hyoid arch** and becomes metamorphosed into the hyoid bone; and the three remaining arches are the **first**, **second**, and **third branchial arches** respectively.

The gill-clefts remain open for a short time only and then close, the gill-pouches subsequently disappearing. The first pouch (hyo-mandibular), however, appears to persist and to give rise to the Eustachian canal of the adult bird; the tympanic membrane appears to arise from the membrane that closes the outer end of the pouch.

The portion of the mesenteron behind the pharynx becomes the

œsophagus (Fig. 92, B, AL); it is a narrow cylindrical tube, at first short, but rapidly lengthening as the neck elongates.

The **stomach** arises on the fifth day as a slight dilation at the end of the œsophagus, and a few hours later its distal end thickens considerably to form the **gizzard**. Behind the gizzard the mesenteron begins to form coils at about the sixth day; from these the different parts of the **intestine** are formed, and from its distal extremity, the **rectum**.

The Liver. The liver arises (Fig. 92, C, L) at the middle of the third day as two tubular diverticula from the intestine a little way behind that portion that will later become the gizzard. The two diverticula do not arise simultaneously, but nearly so. By the end of the third day they have come into relation with the large median vein (meatus venosus) formed by the union of the two vitelline veins (V.V). The hypoblastic cells of the two liver diverticula proliferate rapidly, and grow out as solid branching processes round the meatus venosus. From the mesoblast (splanchnopleuric) (M) that surrounds the diverticula and its branching processes there arise blood capillaries, which thus anastomose freely among the liver processes, and later open into the meatus venosus. The trabecular network of hypoblast cells gives rise to the hepatic cells of the liver, and the cæcal diverticula, by almost infinite branching to the hepatic ducts; the basal portion of the diverticula forms the two bile-ducts of the adult, and from the right of one which the **gall-bladder** arises as a sac-like outgrowth.

The Pancreas. This organ arises as three diverticula from the intestine, just behind the liver diverticula. They arise one at a time, and persist as the **three pancreatic ducts** of the adult bird. The pancreas is formed by the mass of tubules derived from the repeated branching of the primary diverticula, and the blood-vessels and connective tissue from the splanchnopleuric mesoblast.

The Allantois. The allantois is a vascular sac that comes into contact with the egg-shell and performs a respiratory function. It arises on the third day (Fig. 96, A) as an outgrowth from the posterior extremity of the mesenteron (G), and, like all outgrowths of this nature, is covered with a thin layer of the splanchnopleuric mesoblast (M). It grows rapidly and becomes very vascular, and by the end of the fourth day it has grown beyond the embryo, turning dorsalwards in the space between the true and false amnion (Fig. 96, left-hand lower figure). The blood-vessels anastomosing upon its surface are derived from the **allantoic arteries**, which are paired vessels arising from the aorta;

from these the blood is returned by the **allantoic veins** to the vitelline veins just before these enter the liver.

At the close of incubation the allantois shrivels up and disappears. In the frog it never extends beyond the embryo, and persists throughout life as the **allantoic** (so-called urinary) **bladder**.

The Lungs. The lungs arise on the third day as an unpaired and median outgrowth of the ventral surface of the œsophagus, just behind the last gill-pouch. This unpaired diverticulum at its free extremity divides into two, and these in turn branch repeatedly; from these latter, arborescent outgrowths arise and give rise to the spongy substance of the lung; the air-sacs—characteristic organs of birds—are dilations of the terminations of the principal branches. The first two branches formed from the unpaired primary diverticulum become the **bronchi**; the **trachea** arises partly from the primary diverticulum, but mainly from the ventral portion of the œsophagus as far as the origin of the pulmonary outgrowth, becoming constricted off from the dorsal part by lateral folds of the œsophageal wall. The primitive trachea lengthens with the elongation of the neck.

III. The Mesoblastic Organs.

THE SKELETON.

Vertebral Column [1].

The vertebral column in the chick arises from the ventral portion of the primitive somites or myomeres of the body (Fig. 91, MY). After the muscle plates (Fig. 95, P) have separated off, at the end of the second day, the somewhat loosely-packed cells of the ventral portion of the somites grow upward, downward, and inward, surrounding both the nerve cord and notochord (Fig. 95, C, P). The successive mesoblastic segments then fuse together and form a continuous tube, which invests the whole length of the spinal cord and notochord; this constitutes the **membranous stage** in the development of the vertebral column. At the fifth day the tube becomes cartilaginous along the length of the sides of the notochord, while that in the region of the spinal cord develops paired cartilaginous plates, which quickly fuse with the cartilaginous tube surrounding the notochord; the cartilaginous plates give rise to the **neural arches**, and the regions in which they

[1] The student will find the study of the skeleton easier if he first considers that of the mesoblastic somites, post, p. 339.

are formed are designated **vertebral regions** to distinguish them from the regions which lie between them, and which are called the **inter-vertebral regions**. A little later (end of fifth day) the vertebral regions of the notochordal cartilaginous tube become distinguished from the intervertebral ones by greater histological differentiation; and a little later each intervertebral region becomes split into two plates, of which one becomes attached to the hinder vertebral ring, and the other to that in front. Thus the vertebral column is now definitely segmented, and each segment forms a **vertebra**.

The plane of segmentation of the vertebral column, however, does not coincide with that of the mesoblastic somites (proto-vertebræ) (Fig. 91, MY) from which they arose; hence the vertebral segmentation is not the primitive one, but a later and secondary one.

On the sixth day the centra of the vertebræ begin to grow inwards upon the notochord, constricting it and ultimately bringing about its total disappearance. On about the twelfth day ossification sets in; there are in each vertebra three centres from which it starts: one in the centrum and one in either side of the neural arch.

THE SKULL[1].

The mesoblast around the brain (Fig. 96) becomes dense by the aggregation of cells, which are round and not stellate like the cells of the ordinary mesoblast. Within this condensed tract of mesoblast cartilage develops, and first appears about the sixth day.

On either side of the notochord there appear at about this time two cartilaginous bars, called the **parachordal plates**; these underlie the mid- and hind-brains, and with the notochord form a supporting floor for the brain. The parachordal cartilages become extended forwards in front of the pituitary body as short and slender rods, the **trabeculæ cranii**; beneath the fore-brain these unite to form the **ethmoidal plate**. A little later (eighth day) the **basilar plate** is formed by fusion of the parachordals with each other and with the notochord, and their side walls grow up to form the side walls of the skull.

The auditory capsules appear at the sixth day, at the hinder end of the parachordal cartilages, and with which they are fused from the beginning; they grow up around the internal ear.

[1] The student will facilitate his study if he refers back to the description and diagrams of the development of the dogfish's skull, ante, p. 55.

The olfactory capsules are formed at the anterior end of the ethmoid plate in the mesoblast surrounding the epiblastic olfactory involutions.

Towards the end of the eighth day the **inter-orbital plate** arises from the dorsal surface of the ethmoidal plate; it supports the fore-brain in the embryo; from it later the alisphenoid, presphenoid, mesethmoid and inter-orbital septum (orbito-sphenoid) will arise.

The lower jaw and the part of the skull (quadrate) with which it articulates arise from the mandibular arch. As far as is known the development of this arch, as of all the three visceral skeletal arches, is much abbreviated. Two cartilages, which are independent of each other from the first, appear: of these, the dorsal one lies just in front of the auditory capsule and becomes triradiate, and forms the **quadrate cartilage**; the ventral one is much more slender and is disposed forwards, and is called **Meckel's cartilage**; round it later the membrane bones of the lower jaw are formed.

The hyoid bone is formed in part from the **hyoid arch.** This consists of a dorsal slender rod that forms the **columella** of the ear, and which later fuses with one of the auditory ossicles called the stapes; and of a ventral portion, from which arises the **basihyal** and **cerato-hyal** (anterior cornu) of the hyoid bone.

The skeletal branchial arch, like the preceding one, is very incomplete, and only one is represented in the chick. It consists, on either side, of a bar of cartilage, the **cerato-branchial**, meeting in the middle line the median **basibranchial**; the cerato-branchial becomes the posterior cornu of the hyoid.

The Organs of Circulation.

The course of the circulation at the end of the fourth day. The development and relation of the blood-vessels will be more easily understood if a knowledge of the circulation is first obtained.

By the third day the heart of the chick is an S-shaped tube (Fig. 91, D) and is vigorously contracting; it is partially divided into four chambers (S.V, AU, V, TR), the sinus venosus, atrium, ventricle, and truncus arteriosus, by three shallow constrictions. Opening into the sinus venosus by a common aperture are the two vitelline veins (V.V), bringing the blood from the vessels on the surface of the yolk-sac (Fig. 96, Y). Arising from the anterior end of the ventricle is the truncus arteriosus (TR), which lies in the mid-ventral line between the

branchial arches ; it almost immediately divides into two, from each of which there are given off three branchial vessels (aortic arches) that encircle the pharynx, and passing between the gill-slits (Fig. 91, A) enter the two dorsal aortæ (AR). The latter vessels arise early on the second day, and at first are paired along their whole length (Fig. 95, D.A) ; on the third day they are widely separated in the head, while in the body they are fused to form a single vessel for a short distance in the region of the heart, but behind this point they remain paired to their hinder extremities. Each aorta gives off a large artery, the **vitelline artery** (Fig. 91, V.A), which passes out to the area vasculosa of the blastoderm, where it splits up into a meshwork of capillaries, the blood in which absorbs the nutritive material of the yolk. The capillaries by their reunion form the factors of the **vitelline veins** (V.V) which carry the blood to the heart again, thus completing the circulation.

Up to the end of the third day the blood is thus wholly concerned in absorbing nutritive material from the yolk, which it carries to the heart, whence it is distributed to the body. But, by the fourth day, a special respiratory organ is beginning to develop ; this is the allantois (ante, p. 318), and simultaneously with its development paired **allantoic arteries** and **veins** arise. The allantoic arteries arise from the aortæ, and from the first the left artery is the larger of the two, ultimately becoming the sole one, as the right one disappears ; they branch on the surface of the allantois, and the reunion of their capillaries forms the factors of the allantoic veins. These unite immediately after entering the embryo and form a single vessel, which enters the left vitelline vein just before that enters the heart.

At the end of the fourth day, therefore, the allantoic veins are returning oxygenated blood to the heart, and the vitelline veins blood which is laden with nutritive material. Towards the end of incubation the allantois becomes an excretory as well as a respiratory organ.

Within the embryo, at the second day, there are developed two pairs of longitudinal veins, one posterior and the other anterior ; these are the **posterior** (Fig. 95, PC) and **anterior cardinal veins** respectively. The anterior cardinal veins lie in the sides of the head and return the blood thence to the heart. The posterior cardinal veins lie on either side of the aorta, and dorsal to the Wolffian bodies (W) with which they are intimately associated ; they return the blood from these organs and the hinder part of the body to the heart. At the level of the sinus venosus the anterior and posterior cardinals on either side

unite and form a short vein, the **Cuvierian vein**, which enters the sinus venosus.

During the fourth day small veins arise in the wall of the intestine, and by the union of these a median **mesenteric** (sub-intestinal) **vein** is formed, which carries the blood from the intestine to the left vitelline vein, which it joins at the junction of that with the allantoic vein. On the fourth day also a median vein arises between the Wolffian bodies ; this is the **posterior vena cava**. At this stage it is very small and unimportant, but later it becomes intimately related with the definitive kidneys upon their formation. It arises in the mesoblast at the hinder end of the Wolffian bodies and grows forwards to open into the confluent portion (**meatus venosus**) of the two vitelline veins, just behind the sinus venosus.

The Heart. The heart is not formed until at about the commencement of the second day, when it appears as a double tube, formed by the meeting in the middle line, beneath the pharynx, of the two vitelline veins ; at first the two tubes are quite distinct, but before the end of the second day their opposed walls have disappeared, and the cavity then becomes a single one (Fig. 91, B, H). At this stage, about the middle of the second day, the heart is a single, short, straight tube, receiving the two vitelline veins (V.V) behind, and in front passing into two arteries, which later become the first (mandibular) aortic arch, and which represent the anterior part of the two tubes of which the heart was originally composed. Examination of transverse sections of the heart at this stage (Fig. 92) shows that it consists of two layers : an inner, very thin, endothelial one (H), and an outer thicker one of mesoblast cells (ML) derived from the splanchnopleuric layer, and which later becomes differentiated into the muscular substance of the organ ; between these two layers there is at first a considerable space filled with mucus. There is some uncertainty as to the origin of the endothelial layer ; it probably arises, like the endothelium of the blood-vessels in the chick (but not in other Vertebrates, in which it arises from mesoblast), from the hypoblast. The heart is attached along its whole length to the ventral surface of the pharynx by a median membrane derived from mesoblast.

At about the thirty-sixth hour the attachment of the heart along the ventral surface of the anterior part of the gut becomes reduced to two parts, one at either extremity ; between these two points the heart is unattached. By more rapid growth than the part of the embryo to which it is attached, the heart becomes thrown into an ∽-shaped fold

(Fig. 91, C) towards the close of the second day ; that part of the heart which will later constitute the temporary sinus venosus lies on the first limb, that which becomes the atrium (AU) on the first loop, that which will be the ventricle (V) on the second loop, and the truncus arteriosus (TR) on the second limb of the ∽.

On the third day three constrictions have appeared, partially dividing the heart into the four chambers just mentioned (Fig. 91, D).

On the fourth day very important changes occur. Up to this time the heart is a continuous tube, with a single cavity throughout, but on the fourth day the atrium and ventricle each become divided into two chambers. The inter-auricular septum arises from the antero-dorsal wall of the atrium and grows backwards and downwards, dividing the atrium into two auricles ; the inter-ventricular septum arises from the ventral wall of the ventricle and, by dorsal extension and fusion along its dorsal margin with the dorsal wall, divides the ventricle into two chambers.

On the fifth day the truncus arteriosus becomes divided into two chambers by a longitudinal partition, spirally disposed in such a way that the right ventricle of the heart communicates with the fifth aortic arches alone, and the left ventricle with the remaining aortic arches only (ante, p. 115). By the end of the fifth day the septum has fused at its hinder margin with the anterior extremity of the inter-ventricular septum, so that later, at the time of the metamorphosis of the aortic arches, the right ventricle communicates with the pulmonary (fifth aortic) arteries alone, and the left with the systemic (third aortic) arch and its branches (first, second, and third aortic).

The chick thus differs from the dogfish, frog, and rabbit in the possession of five instead of six aortic arches, and in that its pulmonary arteries are derived from the fifth and not the sixth of these. We must remember, however, that until quite recently the rabbit was thought to have only five arches. It is now known that there are six, but the fifth of these is very small and transitory and was consequently long overlooked. And perhaps the fifth arch of the chick really represents the sixth.

The Aortic Arches[1].

The five **aortic arches** (Fig. 91, just behind A.A) of either side arise from the two branches into which the truncus arteriosus (TR) divides; of these arches the first appears at the beginning of the

[1] Compare tabulation of arterial system (p. 116).

second day and lies in the mandibular visceral arch; the second appears by the end of the second day and lies in the hyoid arch; the third, fourth, and fifth appear on the third and fourth days and lie in the first, second, and third branchial arches respectively.

Of the aortic arches the ventral portion of the mandibular and hyoidean becomes the mandibular or lingual arteries of the adult, while the dorsal portion, permanently retaining its dorsal aorta connexion with the third arch, becomes the **carotid artery**; this later branches and forms the **internal** and **external carotids**. The third arch gives rise by outward extension, and by loss of its dorsal connexion with the fourth arch, to the subclavian (pectoral) arteries. Of the fourth pair of arches the left one disappears, the right remaining as the **aortic arch** and permanently retaining its connexion with the dorsal aorta. The fifth pair of arches becomes the **pulmonary arteries**, and by the formation of the longitudinal spiral septum in the truncus arteriosus, described above, opens into the right side of the heart alone. This portion of the truncus forms the root of the pulmonary arteries.

The Origin of the Blood-vessels.

The blood-vessels first arise on the first day in the extra-embryonic portion of the blastoderm situated between the area pellucida and area opaca, and known as the **area vasculosa**. From the upper surface of the hypoblast in this region there are produced a number of anastomosing ridges that are at first solid; later they become hollow and constricted off from the hypoblast, and then form a series of hollow branching tubules lying between the mesoblast and hypoblast. These become invested with a mesoblastic layer, in the process of which they become embedded in the mesoblast. The hypoblastic inner coat becomes the endothelium of the arteries and veins, and forms the capillaries; the mesoblastic layer becomes converted into the elastic, muscular, and fibrous elements of the walls of both arteries and veins. The blood-vessels that arise later, on the second day, within the area pellucida and the embryo are formed in the same way.

The hypoblastic origin of the endothelium of the blood-vessels is, so far as is known, peculiar to the chick, since in other Vertebrates the whole of the constituents of the circulatory organs arise from the mesoblast; the difference, however, is not an important one, since the mesoblast (the primitive streak excepted) in the chick arises from the hypoblast.

THE RENAL ORGANS.

The renal organs of the chick consist of a **head-kidney** or **pronephros**, a **mesonephros**, and a **metanephros**. Of these the first is vestigial and transitory, the second is the functional organ of the embryo, and is very large during this period, while the third develops late and becomes the permanent renal organ of the adult.

The Pronephros. Unlike the order of events in other Vertebrates, the pronephros does not arise in the chick until after the Wolffian (mesonephric) body; but as it is phylogenetically the older organ it will be described first.

It arises at the end of the fourth day as three pairs of peritoneal, pit-like involutions (Fig. 95, G), at the level of about the eighth somite. The involutions lie one behind the other, and are connected by a ridge-like thickening of the peritoneum; this ridge extends backwards beyond the third pit as a rod-like body, lying to the outer side of the Wolffian duct, and later, becoming hollow, forms the anterior portion of the **Müllerian duct**. Up to the fourth day the head-kidney thus consists of three tubular involutions of the peritoneum, opening by their dilated ends into the cœlom, and at the other communicating with the Müllerian duct (D), which ends blindly behind. On the fifth day the two hinder tubules close and disappear, and the Müllerian duct extends backwards rapidly, lying in contact with the Wolffian duct, by the proliferation of the cells of which it is said by some to take its origin in its posterior region (Fig. 95, D, E, F). The first tubule remains as the cœlomic opening (G, D) of the Müllerian duct, which in the female acquires an opening into the cloaca, and subsequently becomes the oviduct.

Wolffian Body and Duct. The Wolffian duct (Fig. 95, A, W) arises on the second day as a ridge-like thickening of that part of the mesoblast which lies between the somite (MY) and the lateral plate (M′ & M) and called the **nephrostome**. On the second day, owing to the position occupied by the nephrostome, the ridge lies immediately beneath the dorsal epiblast (E). It gradually extends forwards, but more rapidly backwards, with the growth of the embryo, and begins to be constricted off from the mesoblast (Fig. 95, B, W). At about the fortieth hour it thus lies between the mesoblast and epiblast as a solid, rod-like tract of cells, extending from the fourth to the fourteenth somite; at about this stage it acquires a lumen and becomes a tube, and a little later, by the rapid extension of the mesoblast, which

grows between it and the epiblast, it becomes embedded within that (Fig. 95, C, W). It gradually continues to grow backwards, and by the end of the fourth day it opens into the cloaca from the dorsal surface.

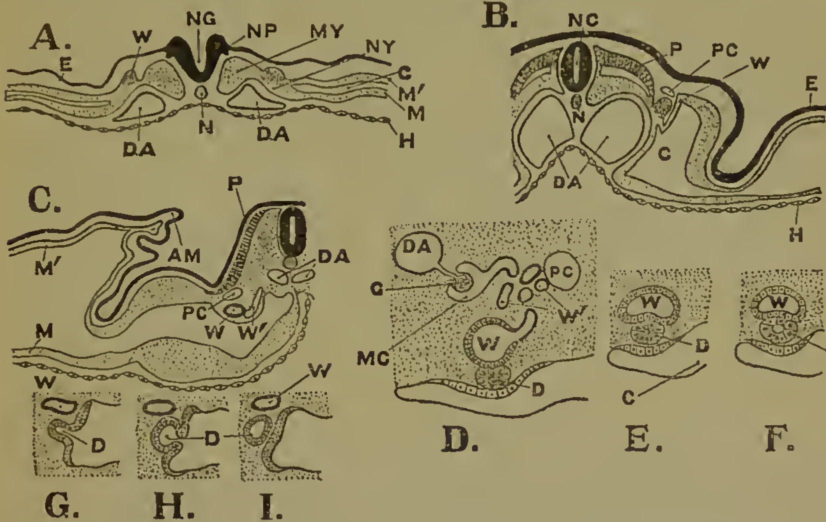


FIG 95. Transverse sections through different regions of the Chick embryo. A. 32 hours; through the seventh somite, showing the formation of the nervous system by the upfolding of the neural folds on either side of the neural groove (NG), and of the spinal nerves by the development of the neural ridge (NP) The mesoblast with its division into myotome (MY), nephrostome (NY), and lateral plate (M & M′) is well shown. The lateral plate has split and formed a cavity (cœlom, C) between two layers, somatopleure (M′) and splanchnopleure (M). The Wolffian duct (W) is just beginning to form as a thickening of the nephrostome, and the post-cardinal vein (PC) is arising just dorsally to it. B. 46 hours; showing the incipient constriction of the Wolffian duct (W) from the mesoblast and the gradual invasion of that upwards and over it. At this stage the neural folds have met and coalesced by their margins, so that the neural groove is converted into a neural canal (NC). C. 70 hours; the Wolffian duct and post-cardinal vein (PC) are now embedded within the mesoblast and the Wolffian tubules (W′) are arising as hollow vesicles in that. The formation of the amnion (AM) by the upgrowth of the epiblast and somatopleure layer of mesoblast is also shown D, E, F. 6–7 days; shows the formation of the posterior end of the Müllerian duct (D) as a thickened tract arising from the proliferation of cells from the Wolffian duct (W), with the subsequent formation of a lumen. In D is also shown the formation of a Malpighian capsule (MC) by indenting of the terminal portion of a Wolffian tubule (W′) by the glomerulus (G) derived from the aorta. The student must bear in mind that a transverse section passing in one plane will cut across a convoluted tubule, like the Wolffian tubules, several times and in various directions. Hence in the section the tubule does not appear as such, but as circular, oval, or elongated spaces. G, H, I. 4 days; shows the formation of a pronephric tubule in G, and of the anterior portion of the Mullerian duct as a thickening of the cœlomic epithelium, and subsequent invagination to form a tube in H and I. AM = amnion; C = cœlom; D = Müllerian duct; DA = dorsal aorta; E = epiblast; G = glomerulus; H = hypoblast; M = splanchnic (visceral) layer of mesoblast; M′ = somatic (body) layer of mesoblast; MC = Malpighian capsule; MY = myotome or somite; N = notochord; NG = neural groove; NP = neural ridge; NC = neural canal (central canal of adult spinal cord); NY = nephrostome; P = muscle plate; PC = post-cardinal vein; W = Wolffian duct; W′ = Wolffian tubules.

The Wolffian body may be divided in the chick into an anterior smaller and a posterior much larger portion: these two portions are distinguished by a slight difference in their mode of origin. The anterior portion, which lies in front of the sixteenth segment, arises as

a number of funnel-like depressions in the peritoneal epithelium, which become connected with solid, cord-like masses of cells in the adjacent mesoblast; these soon become tubular and communicate on the one hand with the peritoneal funnels and on the other with the Wolffian duct. The anterior portion soon undergoes degenerative changes and disappears.

The posterior portion, extending from the sixteenth to the thirtieth somite, arises by the development of oval vesicles in the mesoblast (Fig. 95, C, W′), which by elongation become tubular in form. These form the **Wolffian tubules** (Fig. 95, D, W′); they soon acquire an opening into the Wolffian duct (W), and dilate at their opposite extremities to form globular sac-like structures (MC), which become pushed in by the invasion of tufts of capillaries (G) derived from the dorsal aorta. Each sac-like body is a **Malpighian capsule**, and the tuft of capillaries which it encloses is a **glomerulus**; and it follows from its mode of formation that the cavity between the two layers of the Malpighian capsule is continuous with that of the tubule, so that any material excreted from the capillaries of the glomerulus into the cavity of the Malpighian capsule passes into the tubules, thence by the Wolffian duct to the cloaca. The Wolffian tubules of both the anterior and posterior portion of the Wolffian body lie in close relation to the posterior cardinal vein (PC).

The Wolffian body in both sexes undergoes almost complete retrogression: in the male a small portion persists as the **epididymis**, while tubular outgrowths of the tubules of this region reach the testis and become the **vasa efferentia**; and in the female a vestige, called the **parovarium**, alone remains, lying between the ovary and the permanent kidney. The Wolffian duct becomes the vas deferens in the male, and disappears completely in the female.

The pronephros disappears in both sexes. In the male the Müllerian ducts never reach the cloaca, and completely disappear; in the female the right duct disappears, the left becoming the **oviduct**.

The Permanent Kidney or Metanephros; and its Duct or Ureter. Along the region of the posterior end of the Wolffian duct, from somite thirty to somite thirty-four, the Wolffian body does not extend, and it is in this limited region that the metanephros arises. The metanephros really arises, in part at least, from its duct or ureter, and it is in virtue of this fact that it differs from the mesonephros, and cannot, therefore, be regarded as a posterior extension of that. Towards the end of the fourth day the **ureter** arises on either side

as a diverticulum of the dorsal surface of the hinder portion of the Wolffian duct; it is forwardly directed, and from it lateral tubular outgrowths arise which become connected with strands of mesoblast cells adjacent to them. From these lateral outgrowths and the mesoblast cells the uriniferous tubules of the adult kidney are developed. The mesoblast, from which the strands above mentioned are derived, appears to be of the same origin as that in which the Wolffian tubules arise, i. e. from the nephrostomes (intermediate cell-mass), and is stated by some to be at first continuous with the mesoblastic blastema, from which the Wolffian body as a whole arises; and in so far as that is true, the metanephros appears to be but a specially differentiated portion of the posterior end of the mesonephros.

At the sixth day the ureters acquire an independent opening into the cloaca.

The Mesoblastic Somites and the Cœlom.

As already described, the mesoblast shortly after its first formation forms a continuous sheet of cells lying between the epiblast and hypoblast, and interrupted only along the middle line of the blastoderm by the notochord. About the twentieth hour the mesoblast becomes separated into two distinct layers, an upper and lower (Fig. 95, M′, M) separated by a cavity (C); the upper layer (M′) lies beneath the epiblast, with which it is in parts in contact, and the lower (M) immediately above the hypoblast. Of these the upper layer is called the **somatopleure** and the lower the **splanchnopleure**, while the cavity becomes the **cœlom** or **body cavity**. A body cavity may arise in one of two ways: it may arise, as in the chick, by splitting of the mesoblast into two layers, when it is called a **schizocœl**, or, as in *Amphioxus*, Echinodermata, *Balanoglossus*, and Brachiopoda, from hollow outgrowths of the enteron or primitive alimentary canal, when it is called an **enterocœl**.

The somatopleure with the epiblast forms the body-wall, and the splanchnopleure with the hypoblast the wall of the alimentary canal.

About the twenty-second hour the mesoblast on either side of the notochord becomes divided by a number of vertical clefts, extending outwards for a short distance only from the notochord; these are followed by two longitudinal clefts, one on either side of the embryo, and also vertical. The latter clefts divide the mesoblast of either side into a tract related to the notochord and called the **vertebral plate**, and a more extensive one without this designated the **lateral plate**.

The vertebral plate is by transverse vertical fissures cut up into a number of cubical blocks, the **mesoblastic somites, myomeres,** or **proto-vertebræ** (Fig. 91, MY). The somites extend along the whole length of the embryo, the head region excepted; at first they are few in number, and first appear in the neck region, but by the end of the second day there are nearly thirty pairs present, and they regularly increase as the embryo grows.

The somites are from the first hollow bodies, and their walls of uniform thickness; but by the second or third day (Fig. 95, B) their ventral wall has become much thicker than the dorsal (P), as the result of which the cavity of the somite becomes displaced dorsalwards. The dorsal wall of the somite undergoes a marked histological change and assumes an epithelial character, its individual cells becoming columnar in form; by the end of the third day it has separated off from the ventral part of the somite and constitutes the **muscle-plate** (P). From the muscle-plates the muscles of the back and body are later developed. The ventral portion of the somites becomes converted at an early stage into metamerically arranged segments of muscles, the fibres of which are longitudinally disposed; these muscles are comparable to the longitudinally arranged muscles of fishes and *Amphioxus*, which are similarly metameric; from them, at a later period, some of the muscles of the body are derived, in the process of which their metamerism becomes lost.

The cavity of the somites must be regarded as part of the cœlom[1], and in fact, at the moment of their formation, the cavity of the first two or three somites is continuous with that of the body cavity, but early loses its connexion with that.

At about the thirtieth hour the portion of the mesoblast that lies between the vertebral and lateral plates forms a thinner sheet connecting the two; from this part the Wolffian tubules (nephridia) later arise, and it is hence called the **nephrostome**, in preference to the older term, **intermediate cell-mass.**

The Amnion.

The amnion is a double-layered membranous fold (Figs. 95 & 96, AM) that arises from the blastoderm all round the embryo, and by the end of the fourth day completely envelops it. It is not a permanent structure and is ruptured at the time of hatching.

[1] Refer to p. 276, 'Comparison of Vertebrate and Invertebrate genital ducts, nephridia, and cœlom.'

The embryos of fishes and Amphibia do not possess an amnion, while those of reptiles, birds, and mammals do. Hence the two former classes are grouped as the **Anamnia** and the three latter as the **Amniota**.

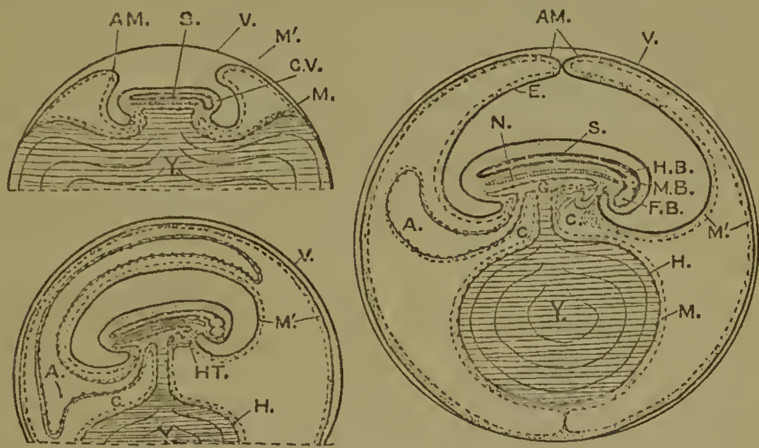


FIG. 96. Diagrammatic representation to show the relation between the embryo and the egg, and between it and the amnion, allantois, and yolk-sac. The top left-hand figure represents the upper half of the egg at between the second and third days of incubation, when the amnion (AM) is well developed, the greater portion of the neural groove (S) is closed, the notochord (N) is definitely formed, but the hypoblast (H) is not yet constricted to form the alimentary canal, but is spread out over the surface of the yolk (Y).

The right-hand figure is a later stage, between the third and fourth days, when the amnion folds (AM) have reached the mid-dorsal line and are about to coalesce, and the allantois (A) has arisen from the gut and turned dorsalwards beyond the embryo. The hypoblast (H) is now much constricted and the alimentary canal is a closed tube opening at one part of the yolk-sac (Y) by a tubular canal, called the yolk-stalk, lying between C—C. The heart is also far advanced; it lies just above and to the right of the right-hand C, and beneath the gut (G). The cranial flexure is pronounced, and the fore- (F.B), mid- (M.B), and hind-brains (H.B) are distinctly marked off. The yolk-sac is much reduced, and is completely invested by the blastoderm (H, M, M').

The left-hand lower figure represents a still more advanced stage, about the sixth to seventh day, when the allantois has spread upwards between the true and false amnion, and also partly downwards. The folds of the amnion have coalesced (end of fourth day), as a result of which there is an inner investing layer, the true amnion, and an outer adherent to the vitelline membrane (V), the false amnion. The yolk-sac is much smaller.

In all three figures it can be seen that the cœlom (C) is continuous with the cavity between the true and false amnion.

A = allantois; AM = amnion; C = cœlom; C.V = cerebral vesicle; E = epiblast; F.B = fore-brain; G = gut or mesenteron; H = hypoblast; HT = heart; H.B = hind-brain; M = splanchnopleure layer of mesoblast; M' = somatopleure layer of mesoblast; M.B = mid-brain; N = notochord; S = spinal cord; V = vitelline membrane; Y = yolk.

The first indication of the development of the amnion is the formation of a crescentic fold of the blastoderm in front of the head, at about the thirty-third hour. This region of the blastoderm, at this stage, is composed of epiblast and hypoblast alone, the mesoblast not yet extending as far. The **head-fold of the amnion**, as this first-formed fold is called, is constituted by an upfolding of the epiblast, the hypoblast taking no part in its formation. During the second day the mesoblast grows in between the two layers of the fold, and the fold

itself extends backwards to the neck region of the embryo. By the end of the second day a tail and two lateral folds (Fig. 95, AM) have appeared, but these differ from the head-fold in that mesoblast is a constituent element from the beginning; the mesoblast here, as in the head-fold, is derived entirely from the somatopleure layer (M′), the splanchnopleure (M) taking no part in its formation. The lateral folds then fuse with the head- and tail-folds to form a continuous ridge extending round the embryo, which is higher in front of the head than elsewhere. The amnion rapidly grows upwards and inwards over the back of the embryo, and by the fourth day its free lateral margins have reached the middle line (Fig. 96), and have become confluent with each other.

From the mode of origin of the amnion it will be seen that it consists of two layers, i. e. the epiblast and somatopleure mesoblast, which, by being thrown into the form of a fold, doubles each layer upon itself, and thus makes the amnion four-layered. Shortly after the confluence of the free margins of the amnion these four layers become arranged so as to form two membranes, of which one closely invests the embryo (Fig. 92, AM), while the other lies externally to this. The inner membrane consists of internal epiblast and external mesoblast, while the outer layer consists of internal mesoblast and external epiblast; of these two membranes the former is called the **true amnion**, and the latter the **false amnion** (Fig. 96).

The space between the true and false amnion is, from its mode of origin, necessarily continuous with the cœlom or body cavity of the embryo (Fig. 96, C). At first it is very narrow and is filled with liquid, but it very soon becomes much wider by the increase in the quantity of the amniotic liquid. The true amnion is continuous with the body-wall of the embryo (Fig. 96), while the false amnion, which lies immediately within the vitelline membrane (V), fuses with that, and peripherally is continuous with the mesoblastic layer (splanchnopleure) investing the yolk-sac.

CHAPTER XXI

THE LIFE HISTORY OF THE COCKROACH AND THE BUTTERFLY, AND THEIR CHIEF STRUCTURAL DIFFERENCES

THE cockroach is an insect that lives concealed beneath stones, bark of trees, or leaves during the daytime, and at night wanders forth

in search of food. Its flattened form and firm texture of body are adapted to the mode of life of hiding away in any nook or cranny, or in flattened spaces. Nothing comes amiss to it in the way of food, from decomposing animal or vegetable matter to the daintiest morsel; its strong, serrated mandibles and its firm but flexible maxillæ are powerful auxiliaries adapted to such an omnivorous diet.

A butterfly, on the other hand, flies freely from flower to flower during the daytime, and lives exclusively upon the honey which it collects from the flowers. Not a few butterflies, however, do not feed at all during their perfect (imaginal) state, for they lay their eggs shortly after reaching the imaginal stage and then die. Correlated with this difference in the kind of food, the mouth parts of butterflies and moths are very much modified, and differ markedly from those of the cockroach. In the latter there is a pair of strong, biting mandibles (ante, p. 231) on either side of the mouth, by means of which solid food of all kinds may be broken and triturated and rendered available for reception by the alimentary canal. Behind these are two pairs of maxillæ or foot-jaws (ante, p. 231), which are instrumental in holding and adjusting the food while the mandibles grind and break it. In butterflies the mandible is either absent altogether or else is reduced to a mere vestige; there is no need for a biting organ in an animal that feeds on fluid food. The first maxillæ are much modified, and the palps and blade (lacinia) are absent in nearly all species; the hood (galea) is elongated and very flexible, and its inner surface is grooved so that, when it is opposed to its fellow, they together form a long tube. This tube the insect can coil up and roll away beneath its head. By its means the honey is sucked up from the nectary of the flower into the buccal cavity, and thence to the other parts of the alimentary canal. In the second pair of maxillæ the galea (hood) and lacina (blade) are absent, but the palps are nearly always present, though small in most species; the basal portions are more or less incompletely fused and form a single piece.

The cockroach is an insect whose prevalent mode of locomotion is walking; for such, a freely flexible body is advantageous, and we find that the leg-bearing segments, i.e. the prothorax, mesothorax, and metathorax, are independent and distinct. In the butterflies, on the other hand, the mode of locomotion is by means of flying, so that in them a firm and less flexible thorax is desirable in order to form a rigid basis for the organs of flight, i.e. the wings. And consequently in them we find that the three thoracic segments are more or less

completely fused together, and the prothorax, which does not bear wings, is more or less reduced in size. In the cockroach the legs are very essential organs, and we find that all three pairs are similar and nearly all equally developed, the hind ones being slightly bigger than the others. In many butterflies, on the other hand, the front pair of thoracic legs are much reduced.

In an insect like the cockroach, which creeps in and out of narrow chinks, there is a great danger that unless the wings are protected they may be damaged. And we find that the fore pair of wings are hardened and firm in order to form **wing-cases**, called **elytra**, thus affording protection for the hind-wings, which are soft, membranous, and flexible, and can be folded up like a fan beneath the fore-wings. The elytra are not used in flying. In the butterflies both pairs of wings are thin, membranous, and flexible, and both pairs are used to aid in flying. In both sexes the fore-wings are larger than the hind ones, though the superficial surface of the latter is greater than that of the former.

The whole surface of the body and head of the cockroach is devoid of scales and is quite naked, while that of the butterfly is covered with very numerous flattened and suppressed scales, to the presence of which the colour markings are due.

The gonapophyses of the female cockroach, already described (ante, p. 230), act as **ovipositors**, holding the egg capsule while the eggs are being deposited within it; in the cockroach they are retracted within the abdomen, but in butterflies they are little developed and in some species may be altogether wanting, since these insects simply pass their eggs on to the surface of a leaf.

Embryology. The egg of the cockroach is elongated, and somewhat crescentic in form, with blunted horns. It is surrounded with two coats, an outer dense chitinous one, and an inner thin membranous one, the vitelline membrane. The eggs of moths are globular in form, and those of butterflies flask-shaped, with elegantly sculptured surfaces.

The eggs of insects are **centrolecithal** and **meroblastic**. After fertilization of the egg the segmentation nucleus[1] divides repeatedly, and the nuclei become scattered in the nutritive yolk; they then pass outwards and arrange themselves in a single layer just within the surface of the egg, and produce a cellular membrane investing that. This membrane is the **blastoderm**, and at this stage the embryo is

[1] See chapter on 'Maturation and Fertilization of the Egg.'

practically a hollow sac filled with nutritive yolk; it is called a **blastosphere** and the stage is spoken of as a **blastula stage.** A little later, one portion of the blastoderm—that which corresponds to the future ventral surface of the insect—becomes thicker than the rest; along the middle of this thickened tract a groove is next formed, and this becomes inpushed (invaginated), the margins of the groove at the same time growing forwards towards the middle line. At this stage, therefore, the embryo consists of a double-walled sac, the two walls (the inner and the outer) being widely separated by the nutritive yolk of the egg. Practically, therefore, it is now a **gastrula,** though a modified one. The lips of the blastopore (folds of the invaginated groove) continue to grow towards the middle line and ultimately meet and coalesce, thus giving rise to a tract of cells, which later extends laterally beneath the epiblast, and will later still give origin to the whole of the mid-gut and the mesoderm of the imago. The investing outer part of the blastoderm is now called the **epiblast.** From the epiblast, on either side of the blastopore, there rises up another ridge-like fold, which grows towards the middle line, and coalesces with its fellow of the other side; there is thus derived two membranes covering the embryo, of which the inner one is called the **amnion** and the outer the **serosa.**

Later in development the epiblast becomes divided into segments by the appearance of transverse furrows. These segments are the rudiments of the segments of the body of the adult, and from all of them, the first and last excepted, a pair of buds or appendages will bud out. Of these buds the first pair become the antennæ, the second pair early disappear, the third become the mandibles, and the fourth and fifth become the first and second pair of maxillæ respectively. Thus, if we take into account the first segment, which bears no bud-like appendages, we can see that the head of the cockroach is composed of six segments. The next succeeding three pairs of appendages become the thoracic legs, while the remaining appendages, those on the segments that become the abdominal segments of the imago, disappear, except those on the ninth and eleventh segments, which persist as the stylets and cercopods respectively.

The stomodæum and proctodæum, which give rise respectively to the fore- and hind-guts, arise on the first and hindmost segments as inpushings of the epiblast.

The hypoblast arises from the invaginated portion of cells already mentioned, and within this a tubular canal, the **mesenteron,** extending

from near the stomodæum to the proctodæum, is formed; this is the primitive gut, and will later give rise to the whole of the mid-gut. The stomodæum and proctodæum eventually open into it.

The nerve chain arises as two longitudinal thickenings of the epiblast immediately on either side of the middle line, in which segmental thickenings appear; the first of these form the brain, and the succeeding ones the ganglia of the different segments of the body.

The mesoblast arises from the same tract of invaginated cells that gives rise to the hypoblast. On either side of the hypoblastic strand the mesoblast becomes hollowed out in each segment of the body; these are called the **cœlomic pouches**. In the dorsal portion of these pouches the rudiments of the gonads early appear as large and prominent cells. The remaining portion of the body cavity becomes filled with fat.

The genital passages for the most part arise from the mesoblast; the germ-cells—those that will produce ova or sperm—become surrounded by other mesoblast cells which form tubular channels, and give rise to the tissues and ducts of the testis and ovary. The vagina of the female and the ejaculatory duct of the male arise, like the tracheal (breathing) tubes, as inpushings of the ectoderm.

Gradually all the organs are completed, and all the nutritive yolk-material disappears. The cockroach is then ready to be hatched, and it escapes from the egg capsule by secreting a fluid from its mouth which softens the cement that closes that, and then it pushes its way out. A cockroach just hatched is colourless and possesses no wings, and its sexual organs are very immature. Wings and sexually mature gonads are not attained until the insect reaches its perfect condition. When first hatched the cockroach is much deeper than wide, but a little while afterwards it becomes as much wider compared to its depth, as it was before deeper than its width, and assumes the characteristic flattened form of the adult. After a short while it becomes darker in colour and begins to grow. But its outer chitinous skin does not grow, so that from time to time it has to throw its skin off or **moult**. A moult is technically known as an **ecdysis**. How often the cockroach moults is not certain, but possibly there are five or six before the adult or perfect condition is attained. In the case of our domestic cockroach it is said that the first moult takes place soon after hatching, a second at the end of a month, and five more distributed over a period of five years. But in the case of another species it is said that there are six moults, all of which occur within

six months of hatching. But in any case the wings are not developed, and the sexual organs are not matured, until the final ecdysis has occurred. There appears to be no special period of the year for laying the eggs, since the young can be found at almost all seasons.

The young cockroach, called a **nymph**, is therefore characterized by the fact that at hatching it is very similar to the parent, only differing in those details which we have already mentioned. And it reaches the adult condition mainly by growth and the development of wings.

It is quite otherwise with the butterfly, for the organism that is liberated from the egg at the time of hatching is different to the parent. It is a soft, elongated, segmented creature, called a **larva** or **caterpillar.** There are altogether thirteen segments, of which the first forms the head, and is usually more deeply pigmented than the others; the second, third, fourth, and a part of the fifth, will form the thorax of the adult, and each bears a pair of appendages, which are short and curved in form; the segments behind form the abdomen of the adult, and the seventh to tenth bear each a pair of abdominal legs, which are usually furnished with spines or hooks, and with their free extremities indented to form a sucker-like pad.

The head bears a pair of strong mandibles by means of which the caterpillar devours leaves; it will be remembered that these are reduced to mere vestiges in the imago, or disappear altogether. The two pairs of maxillæ are small and inconspicuous in the caterpillar, though in the imago the first pair become developed into a long sucking tube.

The nervous system of the caterpillar is interesting, since it possesses eleven ganglia, whereas in the imago there are only seven. This reduction is brought about in the pupal stage by the coalescence of the first, second, third, and fourth ganglia of the larva, exclusive of the pair lying in the front part of the head, and which give rise to the cerebral ganglion of the imago. The fifth and sixth ganglia of the caterpillar entirely disappear, or become coalesced with the others.

The alimentary canal, though it does not become that of the adult, is similar to it, and consists of the same parts. The breathing organs are similar to those of the imago, though the stigmata are wanting on the second and third thoracic and on the last abdominal segment.

The business of the caterpillar, which is called the **larva**, is to feed and to grow as rapidly as possible. The larva of the common silkworm is scarcely a line in length when first hatched, and does not weigh more than a hundredth of a grain; but at the end of thirty days

its average weight is ninety-five grains, and its length about forty lines, so that it has increased its weight nine thousand five hundred-fold.

When the larva has attained its full size, it shows evident signs of uneasiness, ceases to feed, and wanders about in search of a place where it may pass into the next stage, that of a **pupa** or **chrysalis.** Having found a place suited to it, it spins a cocoon of silken threads from a pair of 'silk-glands,' consisting of long coiled tubes, often longer than the body in which they lie coiled, and the ducts of which open to the exterior through a tubular spinneret, situated in the mouth. Very often only a silken pad is formed, or the edges of leaves are bound together by the silk fibres so as to form a hollow receptacle. But whichever of these means is adopted the larva comes to rest, and very shortly afterwards it bursts its larval skin near the head end of the body, and gradually wriggles out from it. The outer skin of the pupa then hardens, and within it the wings and thoracic legs are formed and developed. It is at about this stage also that the concentration of the nervous system takes place, and the larval alimentary canal, glands, and air-tubes (tracheæ) break down. This breaking down is a degenerative process, in which the component cells become disintegrated and absorbed by the blood corpuscles; it is known as **histolysis.** The new organs are then reformed by means of **imaginal buds**; these are infoldings of the skin, and the energy required for their development is derived from the food material stored up in the blood corpuscles and the fat-body.

As soon as all the organs are developed the pupal skin separates from the contained tissues within, and splits open in the thoracic region to allow of the escape of the **imago** or **perfect insect.** After liberation from the pupal skin the imago is soft, but soon hardens, and its wings are small and much crumpled; the butterfly liberates itself from the cocoon, in some cases by secreting a solvent from the hind-gut, which weakens the material sufficiently to enable it to force its way out, when it makes its way to a twig, where it rests with the wings hanging downwards; air and blood are carried to them, and they rapidly expand, grow, and become firm.

The chrysalis or pupal stage is thus apparently a quiescent one, for the pupa spends it in a motionless condition within the cocoon; but in reality it is one of great activity, for, as we have seen, the old organs are breaking down and the new ones are being formed. The pupa is therefore neither like the larva from which it came, nor exactly like

the imago into which it will turn; but it becomes less like the larva and more like the imago.

Thus in the life cycle of the butterfly three distinct stages are passed through, but each is intimately related to the other: there is the active **larval stage**, during which the organism is feeding and storing up a reserve of potential energy; there is the apparently quiescent, in reality active, **pupal stage**, during which no feeding takes place, and the potential energy stored up in the previous stage is utilized in the formation of the imago; the **imaginal stage** is that of the perfect insect, which often only lasts a few days, a single day, or a few hours, and the chief, and in most cases the sole, event of which is the fertilization and deposition of the eggs. The deposited eggs remain dormant during the Winter, and develop into the larva in the following Spring, and this will become the pupa, whence the imago will subsequently arise.

Thus the two great series of processes that constitute life, i. e. those protective of the individual and those protective of the race, are in the life cycle of the butterfly divided, and the one series is mainly performed in the one phase and the other series in the other phase. There is, in other words, a **differentiation of labour**, for the processes connected with nutrition and growth are almost wholly restricted to the larval stage, and those of reproduction to the imaginal stage. A grub feeds industriously underground for years in order that a chafer may live a transient period in the upper air. The larva of a Yucca moth feeds continuously on the ovules—and therefore on so many potential Yucca plants—of a Yucca flower, in order that a Yucca moth may live for but a single night while it deposits its eggs. The nymphal and larval stages of May-flies last for years, but the existence of the imago is not for longer than a few hours or days at most. Reproduction, or the maintenance of the species, is the ruling passion of living things, strong in all, and in some instances even unto death.

Insects, in the life history of which there is a resting pupal stage, are said to be **holometabolous**, and their **metamorphosis** is said to be **complete**. In the case of the cockroach, the nymph leads the same sort of life as the imago, and only differs from it in the absence of wings and the immaturity of the sexual organs; it reaches the adult condition by growth and several ecdyses. We have in these cases **gradual metamorphosis** without the formation of distinct stages. In other instances, among primitive insects, the Thysanura and the

Collembola, the larvæ are like the imagines, living the same sort of life and possessing wings; but they are smaller and the sexual organs are not mature, and the attainment of the imaginal condition merely consists in growth and ripening of the gonads. In such cases there is no metamorphosis at all, and the insects are said to be **ametabolic**. Among dragon-flies and May-flies the larvæ are aquatic and the imagines are terrestrial; after several moults the aquatic larvæ become nymphs with an approach to the body form of the imagines and bearing rudimentary wings; the nymph is an approach towards a pupal condition, but is not actually one. Insects in which there is in the life cycle an approach towards the pupal habit without the assumption of a pupal form are said to have an **incomplete metamorphosis**, and to be **hemimetabolic**.

Tabulation of the Chief Differences between the Cockroach and a Butterfly.

Cockroach.	Butterfly.
Head.	**Head.**
The eyes occupy relatively only a small portion of the side of the head. Head is flattened from front to back = elongated from above downwards.	The eyes occupy nearly all the side regions of the head. Head tends to be globular in form.
Head is naked.	Head is covered with flattened hairs = scales.
Antennæ taper to a point.	Antennæ thickened into a club at the tip.
Mandibles are strong biting jaws with serrated edges.	Mandibles are vestigial or absent.
First pair of maxillæ are organs of prehension and adjustment, and consist of several joints: a basal cardo; a stipes, bearing outwardly a segmented palp, and inwardly a hood or galea; and a blade or lacinia.	In the first pair of maxillæ the palps are rarely developed, and the blade is nearly always absent. The hood is long, flexible and grooved, and opposed to its fellow forms a long tube, which can be rolled up beneath the head.
Second maxillæ are similar to the first, but the basal elements (cardo) are fused together.	The palps are nearly always present, and the basal portions are fused to form a single piece. The galea and lacinia are absent.
Thorax.	**Thorax.**
The three segments of the thorax are independent and distinct.	The prothorax is reduced and the thoracic segments are more or less fused together.

Cockroach.	Butterfly.
Thorax.	**Thorax.**
The three pairs of thoracic limbs are similar, and the hinder ones are slightly bigger.	In some butterflies the front pair of thoracic limbs are much reduced.
The fore-wings (elytra) of the female are small and vestigial in *Blatta orientalis*, but not in *Periplaneta americana* or in *Phyllodromia germanica*. In both sexes (when present) they are firm and horny, and act as covers for the hind-wings. The hind-wings are absent in the female of the common cockroach (*Blatta orientalis*), but present in the American and German cockroaches. In the males they are thin and flexible, and used for flying.	The fore-wings are larger than the hind-wings in both sexes. They are thin and flexible, and both fore- and hind-wings are used in flight.
Both pairs of wings are naked (devoid of scales).	Both pairs of wings are covered by multitudinous, flattened, suppressed scales, which give rise to the characteristic coloured patterns of the wings.
Habits.	**Habits.**
Cockroaches live in concealed situations, beneath stones or bark, coming out to feed at night upon all kinds of substances.	Feed entirely on honey which is obtained from flowers, but a large number of adults never feed.
Metamorphosis.	**Metamorphosis.**
The hatched young are similar to the parent, differing in the absence of wings and in the immaturity of the sexual organs. There is thus only a gradual metamorphosis, not distinguished by definite stages.	The hatched young are quite different from the parent, and pass through a larval and a pupal stage before becoming the imago. There is thus a complete metamorphosis, distinguished by definite stages.

CHAPTER XXII

KARYOKINESIS. OOGENESIS AND SPERMATOGENESIS. MATURATION AND IMPREGNATION OF THE EGG. PARTHENOGENESIS

It has already been stated (ante, pp. 5 & 304) that every multicellular animal and plant arises from a single cell, called the **ovum**, by a process of often repeated division. The division of the cell is

preceded by that of the nucleus; and the subsequent division of the former may take place by a simple process of constriction, which commences round the equatorial periphery of the cell and gradually extends inwards to its centre, or by the formation of an equatorial **cell-plate** (Fig. 97, E), which apparently consists of a disc of protoplasm more dense and granular than the rest. The division of the nucleus may be **direct** or **indirect**; in the former case the nucleus is simply split into two, just as an apple may be, while in the latter a series of complicated changes, involving the disappearance of the nucleus as such, precede the actual division. To the series of changes constituting the act of indirect nuclear division we apply the term **mitosis** or **karyokinesis**, and to the act of direct division that of **amitosis**.

If we examine a resting cell just preceding the act of mitosis we shall find that the nucleus has a more or less uniformly granular aspect, with a well-defined **nuclear membrane** (Fig. 97, A. N). In the protoplasm of the cell, lying near the nucleus, is to be seen a round body with radial striations passing outwards from it; this body as a whole is called the **centrosphere** or **astrosphere** (A), and the round body in the centre of the radial striations, the **centrosome** (C). The centrosome is always a definite structure in animal cells, but in plant cells it frequently cannot be distinguished from any of the other granules present, unless by the development of the radial striations. It is thought, therefore, that the centrosome is a dynamical centre, acting as a fixed point for the operation of the forces concerned in the act of karyokinesis; and there are other reasons, as we shall learn in the sequel, for thinking that this is probably its chief function. In most instances there is only a single astrosphere in the resting cell, but in certain algal plants there are two, one at either pole of the nucleus.

The nuclear membrane encloses the **nuclear sap**, a homogeneous unstainable substance, in which is embedded granular particles, which become deeply stained by certain dyes; the granules are collectively spoken of as the **chromatin** (CR), and in the resting nucleus they appear to be uniformly scattered, and in their arrangement to constitute a kind of spongework, the meshes of which are filled by the nuclear sap. There are also present one or more small round bodies, the **nucleoli** (N′), which are deeply stained by aniline and other dyes; by some investigators they have been compared to the micronucleus, and by others to the macronucleus of the Protozoa.

As a rule the first evidence of commencing karyokinesis is the

division into two of the single astrosphere (Fig. 97, B) and the gradual divergence of the two portions; but sometimes the act is fairly well

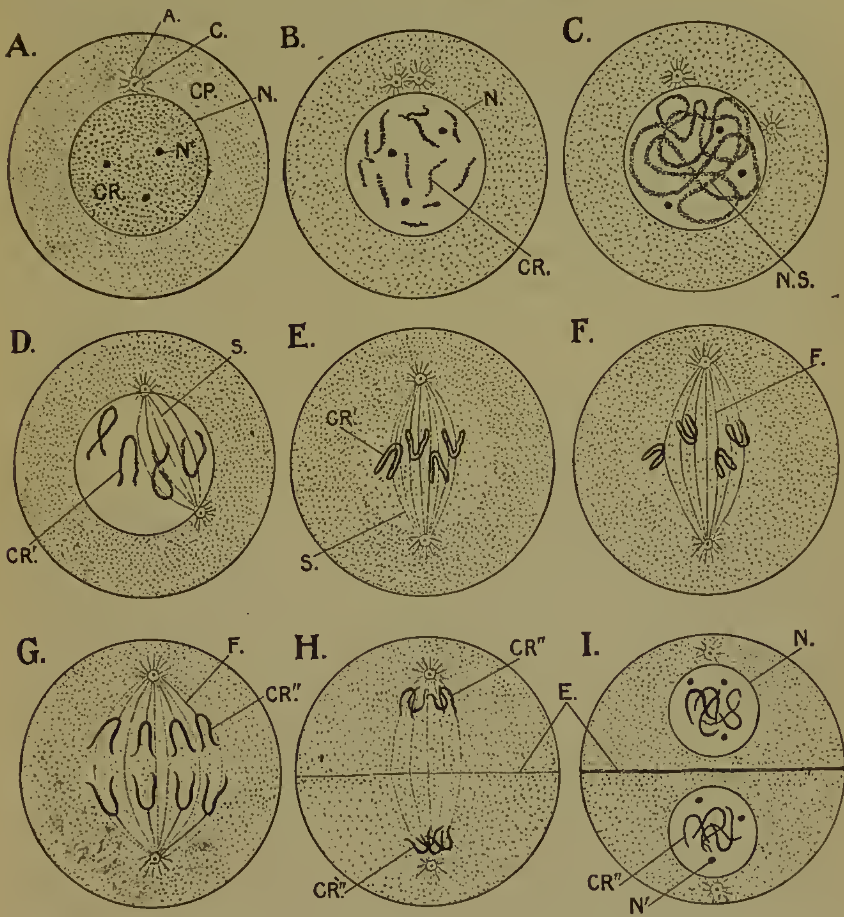


FIG. 97. A series of figures representing in a diagrammatic manner the changes which take place in a typical mitosis or karyokinesis. A. Resting stage of the nucleus. B. Mitosis just commencing: tbe astrosphere divides and the chromatin aggregates into strands or threads. C. The astrospheres diverge and the chromatin strands now form a network, called tbe nuclear skein. D. The formation of the nuclear spindle and the splitting of the nuclear skein into U-shaped fibres, called tbe chromosomes. E. The disappearance of the nuclear membrane and nucleoli, and the longitudinal splitting of the chromosomes. F. The attachment of the split chromosomes to mantle fibres. G. The pulling apart of each half of a split chromosome by the contraction of the mantle fibres. H. The concentration at either pole of the cell of the chromosomes and the formation of an equatorial cell-plate. I. The reappearance of the nuclear membrane and the nucleoli. A = astrosphere; C = centrosome; CP = cell protoplasm; CR = chromatin granules and strands; CR′ = chromosomes; CR″ = the half derived from the longitudinal splitting of a chromosome; E = equatorial cell-plate; F = mantle fibres (fibres of the nuclear spindle to which the chromosomes become attached); N = nuclear membrane; N′ = nucleoli; N.S = nuclear skein; S = nuclear spindle.

advanced before the astrosphere exhibits any change. In the cells where there are two astrospheres no division takes place. In either

instance the astrospheres ultimately take up a position at either pole of the nucleus, and there passes from one to the other a certain number of radial fibres, so that there is formed a spindle-like structure called the **nuclear spindle** (Fig. 97, D, S). While the astrospheres are arranging themselves the chromatin granules increase in quantity and aggregate themselves in tracts of thread-like lines (Fig. 97, B, CR); and very soon after this the chromatin granules are seen to be arranged within the substance of a fibril complicately folded upon itself (C, NS), called the **nuclear skein**. In some cases, as in the nuclei of the salivary glands of *Chironomus*, the chromatin is arranged in the fibrils in the form of regularly alternating discs; but in the majority of instances it is uniformly scattered, giving to the fibril an evenly granular appearance. The fibril next splits into a number of segments, which are numerically constant for the same species, but which may vary in different species from as few as two to as many as twenty-four; these are called the **chromosomes** (Fig. 97, D, CR′). Each chromosome ultimately attains a U-shaped form, and at about the time that the nuclear spindle (S) first develops they begin to arrange themselves in the equator of the nucleus. In the meantime the nucleoli and the nuclear membrane have disappeared, and the nuclear sap has merged with the protoplasm of the cell (Fig. 97, E). The chromosomes then split longitudinally along their whole length (E, F, G, CR′), so that their number is now doubled, and they become so arranged that one of each pair is placed on either side of the equator of the cell (G, CR″). Certain fibres (F) of the nuclear spindle, called **mantle fibres**, are attached one to each chromosome, and after the splitting of the latter they begin to contract and to pull each half of each chromosome towards its respective astrosphere. Thus there begins to be aggregated near each astrosphere (H, CR″), which lie at the poles of the nucleus, a number of chromosomes numerically equal to those which were formed by the splitting of the fibril (nuclear skein). The protoplasm of the cell then either begins to constrict at its periphery, or a plate, the **equatorial plate** (H, I, E), is formed in the equator of the cell; the end result in either case is the same, i.e. the cell is divided into two. The nuclear spindle disappears (Fig. 97, I), the chromosomes in either cell merge together, and the nuclear membrane (N) and the nucleoli (N′) reappear. Thus are formed two cells, each with its own nucleus, the chromatin element of which has been derived from a number of chromosomes numerically equivalent to those of the parent cell.

The above description may be regarded as one of a typical case of karyokinesis, but it does not hold true in detail for all cases. There is, as a matter of fact, a somewhat remarkable range of variation in the details of karyokinesis in different species. In *Fucus* (the Wrack), for instance, a nuclear spindle is not developed, the nuclear membrane persists throughout, and the chromatin aggregates at either pole of the nucleus, instead of in the form of strands or ropes. In the developing spores of Liverworts the chromatin aggregates at the middle of the nucleus, and the nuclear spindle does not appear until late. In *Salamandra* the nuclear spindle is introduced from the protoplasm of the cell, i. e. arises as a differentiated portion of that, but in Liverworts and in *Ascaris* it arises as a differentiation of the nuclear sap (achromatin).

Oogenesis and the Maturation of the Egg.

At a certain period in the embryonic development of every animal the incipient sexual gland (gonad) consists of a mass of undifferentiated cells, so that it is impossible at this stage to say whether the gland will become a testis or an ovary. Leaving *Amphioxus* out of consideration for the present, the sexual gland in the Vertebrata arises, with but one or two exceptions, as a paired ridge formed by a thickening of the cœlomic epithelium on the dorsal wall of the cœlom and to the inner side of the mesonephric tubules. These ridges are called the **germinal ridges**, and though the details of their structure vary in the different classes of the Vertebrata, they essentially consist at first of a mass of similar cells. These are the **primitive sex cells** (Fig. 98, 1), and the nucleus of each contains the same number of chromosomes as those of the ordinary body-cells. The chromosomes and astrospheres then divide (Fig. 98, 2), but without any corresponding division of the cell, so that the nucleus of the cell now contains twice the number of chromosomes that those of the body (vegetative) cells do. This cell is now called the **egg mother-cell**, and from it there is derived a single **egg** or **ovum** (Fig. 98, 3). The egg mother-cells (2) increase in size by the absorption of some of the other cells of the germinal epithelium, which almost from the very first have remained smaller than those destined to become the sexual cells. When the egg mother-cell has attained its full size it becomes surrounded by an **egg-membrane** derived from the egg itself, and by a **follicular membrane** without this, derived from the smaller cells above mentioned, some of which arrange themselves around the egg

in the form of a continuous membrane. There may be more than one egg-membrane present, and usually two may be distinguished: an internal, radiately striated one, the **zona radiata** (Z.R), and an external

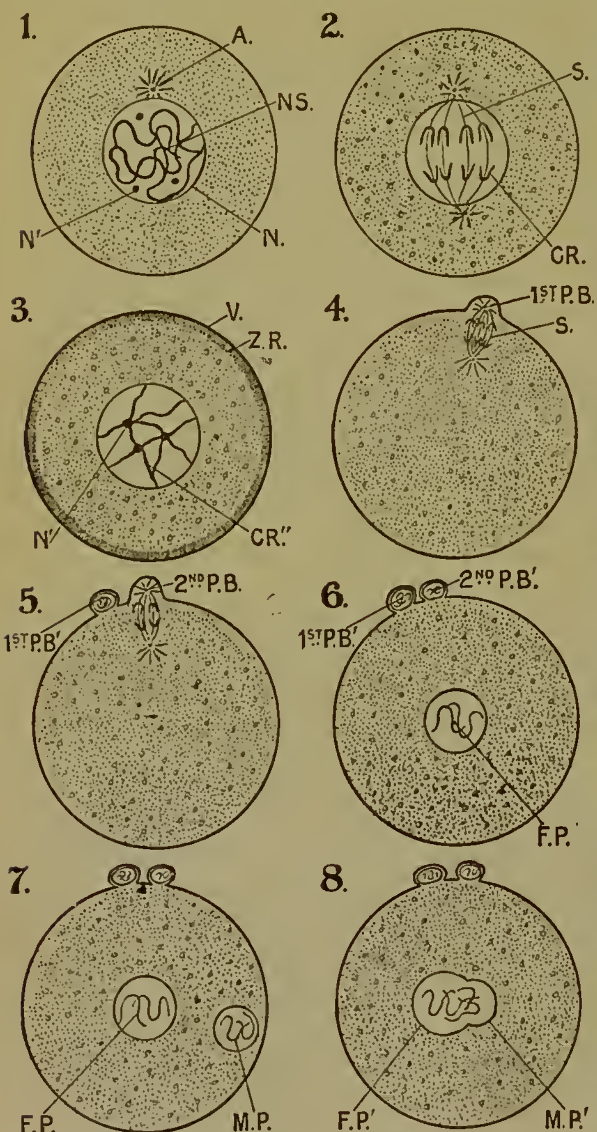


FIG. 98. A series of figures representing the chief stages in oogenesis, diagrammatically represented. The egg-membranes are only represented in 3.

1. Primitive sex cell containing the same number of chromosomes as the vegetative cells of the same individual.

2. Egg mother-cell; in which the chromosomes divide, but not the nucleus or cell; the cell thus contains twice the number of chromosomes of a vegetative cell.

3. Ovum or egg, not yet matured. It is characterized by its large nucleus (called germinal vesicle), and by its radiating chromatin elements equivalent to double the number of chromosomes of the vegetative cells.

4. First stage in the maturation of the egg, consisting in the formation of the first polar body by a reducing division.

5. Second stage in the maturation of the egg, with the formation of a second polar body by a reducing division.

6. The matured egg, with its female pronucleus containing only half the chromosomes of the vegetative cell.

7. Entry of the male pronucleus, constituting the act of fertilization.

8. Fusion of the male and female pronuclei to form the segmentation nucleus and concluding the act of fertilization. The fusion of male and female pronuclei raises the chromosomes to the same number as that of a vegetative cell.

A = astrosphere; CR = chromosomes; CR″ = chromatin strands of germinal vesicle; FP = female pronucleus; FP′ = female pronucleus fusing with the male pronucleus; MP = male pronucleus; MP′ = male pronucleus fusing with the female pronucleus; N = nucleus; N′ = nucleoli; NS = nuclear skein; 1st P.B = formation of first polar body; 1st P.B′ = extrusion of first polar body; 2nd P.B and 2nd PB′ = formation and extrusion of second polar body respectively; S = nuclear spindle; V = vitelline membrane; Z.R = zona radiata.

homogeneous one, the **vitelline membrane** (V); the latter is developed before the former. In the dogfish the zona radiata disappears before the egg is ripe, and the vitelline membrane before the egg reaches the oviduct. In the chick the zona radiata early disappears, but the vitelline membrane persists. In the rabbit a zona radiata and a vitelline membrane are both present; the follicular membrane becomes many-layered and very much thickened at one portion, within which a cavity filled with albuminous fluid is developed. The whole structure is known as a **Graafian follicle**, and the follicle cells as the **membrana granulosa**. In the dogfish, frog, and fowl, the follicular layer remains a single one.

While the egg mother-cell (**2**) has been enlarging and forming its membranes, the protoplasm of the cell has been forming a number of plastic granules, which it deposits within its substance; these granules are nutritive in nature, and serve for the nourishment of the egg during the early stages of its development into the embryo. The **yolk-granules** (Fig. 98), as they are called, may be deposited in great quantity, as in the eggs of reptiles and birds and some fishes, or in less amount, but still in quantity, as in the eggs of the frog, or in very minute quantity, as in the eggs of most mammals and of *Amphioxus*. The nucleus has also become characteristic during these changes of the cell (Fig. 98, **3**); it has become large, has developed one or more prominent nucleoli (N′), and the nuclear sap (achromatin) contains within it the chromatin arranged in strands (CR″), with a tendency to radiate from the nucleoli. The nucleus of the female sexual cell is usually called the **germinal vesicle** and the nucleoli the **germinal spots**.

The egg mother-cell thus enlarged, laden with yolk-granules, covered with egg-membranes and a follicle, possessing a large and characteristic germinal vesicle, the chromatin strands of which represent twice the number of chromosomes of that of the vegetative cell of the same individual, is now called an **ovum** or egg (**3**).

It is now fully formed but not mature; though containing all the essential parts of an ovum it is incapable of fertilization by the male cell. It has yet to undergo certain remarkable changes, the precise significance of which we do not yet clearly understand, and which are spoken of as the ripening or **maturation of the egg**. That which is regarded as constituting the essential feature of maturation is a process of a twice repeated nuclear division, the ultimate purpose of which is a reduction of the number of chromosomes. The germinal vesicle

travels outwards to the periphery of the ovum (Fig. 98, **4**), loses its nuclear membrane, and forms a nuclear spindle (S) and chromosomes; the number of the latter is double that of the ordinary (vegetative) cells of the body, and they differ from those of an ordinary vegetative mitosis in that they do not at this division double their number by longitudinal splitting. The protoplasm of the ovum at the point where the nuclear spindle is situated is protruded outwards in the form of a little knob-like process, into which one pole of the spindle is projected. Upon the separation of the chromosomes and their aggregation at either pole of the spindle to form two daughter-nuclei, one-half of them will be contained within the projection, while the other half will be retained within the ovum. The projection then becomes constricted off from the ovum, and lies between that and the vitelline membrane as a small, round body, called the **first polar body** (**4** & **5**, 1st P.B). The nucleus of the ovum again divides in a similar manner (**5**), by which half of its remaining chromosomes are passed into a **second polar body** (**5** & **6**, 2nd P.B, 2nd P.B′), the remaining half being retained within the nucleus of the ovum. The latter is now called the **female pronucleus** (F.P), and it will be readily understood that, as a result of the changes through which it has passed, it only contains one-fourth of the number of chromosomes of the unripe germinal vesicle; the other three-fourths have been ejected from the ovum into the two polar bodies, i. e. one-half into the first polar body and one-quarter into the second one.

If, therefore, we suppose that we are dealing with a species in which the vegetative cells of the body contain four chromosomes, then the egg mother-cell or unripe ovum will contain eight. At the formation of the first polar body there is no longitudinal splitting of the chromosomes as in an ordinary mitosis, and the result is that the nucleus will now contain one-half the number of chromosomes, and the polar body the other half, i. e. four in each. Thus, at this stage, the ovum and the first polar body are morphologically equivalent each to a vegetative cell. At the formation of the second polar body the number of chromosomes in the nucleus of the ovum are again reduced by one-half, so that the female pronucleus and the second polar body only contain two chromosomes each, and are morphologically equivalent to half a vegetative cell.

The processes of sexual mitosis thus differ from those of the vegetative kind, in that the chromosomes of the nucleus of the primitive sex cell divide once without a corresponding division either of

the cell or nucleus, a process by which they are doubled in number, and in that, in the two subsequent divisions of the germinal vesicle, the chromosomes do not split longitudinally at each mitosis, the result of which is a reduction of their number on both occasions. The two divisions, by which the number of chromosomes are reduced by one-half at each mitosis, are called **reducing divisions**.

The male cells or **sperms** (spermatozoa) arise in fundamentally the same way as the female cells or ova. The germinal ridge destined to become a testis contains primitive sex cells like those of the corresponding germinal ridge of the female. The chromosomes of these become doubled in number and give rise to **sperm mother-cells**, in precisely the same way that the primitive sex cells gave rise to the egg mother-cells. Each sperm mother-cell then divides twice by a reducing division, so that there are produced four cells, each with one-quarter the number of chromosomes of the sperm mother-cell; each of these is a **sperm** or **spermatozoa**. The processes by which the spermatozoa are derived from the primitive sex cells are collectively spoken of as **spermatogenesis**.

The sperm cells undergo great elongation, by which the greater portion of the protoplasm forms a long vibratile **tail**, and the chromatin and astrosphere are lodged in an enlargement at one extremity called the **head**.

Each sperm thus has the morphological value of half a vegetative cell, and is equivalent in respect of the number of its chromosomes to an ovum. **Fertilization** consists in the fusion of the head of the sperm with the female pronucleus; this is brought about by the activity of the spermatozoa, which when discharged into the oviducts of the female, or upon the spawn if fertilization is external, ascend the oviducts or penetrate the substance of the spawn until they reach the eggs. The vitelline membrane of the egg of some species (*Anodonta*) is perforated at a particular spot by a minute aperture, called the **micropyle**, through which the fertilizing sperm may pass; but in other cases the sperm has to wriggle through the egg-membrane, and in certain instances (starfish) the ovum may send out a papilla-like process towards the sperm which first reaches it, and into which the sperm passes. As soon as the head of the sperm has penetrated into the ovum it loses its tail and becomes a rounded, nucleus-like body, which is called the **male pronucleus** (Fig. 98, M.P). It then gradually advances deeper within the ovum, accompanied by its astrosphere (centrosphere), towards the female pronucleus and its astrosphere;

ultimately the two pronuclei fuse (Fig. 98, 8) to form the **segmentation nucleus.** Sometimes the two astrospheres also fuse; but apparently, in the majority of known instances, the female astrosphere degenerates.

The ovum is no longer known by that name, but is now called the **oosperm** or impregnated egg. It is capable of doing that which the unfertilized ovum cannot do, i. e. by a process of rapidly repeated and almost indefinite cell-divisions of the vegetative type, to give rise to an organism identical to that whence the ovum was derived. Thus the oosperm is the first stage in the development of the organism, and it is a **unicellular embryo**, quite unlike in form or structure the parent whence it was derived or the individual into which it will ultimately develop. The nature of the changes which intervene between the oosperm and the fully formed organism are described in the chapter on 'Embryology' (ante, p. 304).

It has already been shown that the female and male pronuclei each contain one-half the number of chromosomes of a vegetative cell; hence it follows that the fusion of the two pronuclei results in two things: the equal contribution of the male and female parent to the formation of the segmentation nucleus, and the restoration of that to the morphological value of a vegetative cell. The segmentation nucleus is thus the nucleus of the first vegetative cell (zygote) of the embryo, and from it will ultimately be derived all the vegetative and sex cells of the mature organism. From the fact that essentially the only portion of the male gamete[1] that enters the egg is the nucleus with its contained chromatin and its centrosphere, and that this is alone concerned with uniting with the female pronucleus, we may infer that the chromosomes—which appear to be the sole object affected by the mitotic rearrangement—are the carriers of the physical and mental characters of the two parents.

PARTHENOGENESIS.

It has already been stated that an ovum cannot develop into an embryo without being previously fertilized by the male cell, and that fertilization is not effective until the maturation of the ovum is completed. But there are certain exceptional cases occurring among insects, rotifers, Bryozoa, crustaceans, and some plants, in which unfertilized

[1] A *gamete* is a sexual cell, male or female, or of indeterminate sex as in conjugation. A *zygote* is the product of the fusion of two gametes.

ova may develop into normal individuals. In certain species of gall-flies and saw-flies the individuals are all females and the males are unknown; consequently the eggs of the females must develop without fertilization. There are also a few Phanerogamous plants in which the males are not known at all, or do not occur within many miles of the female plants, but in which normal seeds are produced. Among saw-flies, moths, fir-lice, plant-lice, and the queen bees, under certain conditions, unfertilized eggs may develop. The parthenogenetic eggs of the queen bee and the gooseberry grub produce male individuals, while those of gall-flies, saw-flies, and plant-lice (Aphides) produce female.

The extreme rapidity of reproduction of plant-lice during the Summer is known to all; such rapid multiplication is possible only by parthenogenetic development. The last batch of eggs laid in late Autumn are fertilized ones, and these remain dormant during the Winter, and in the following Spring develop into females. Since there are no males produced the eggs of the females must develop without fertilization; rapidly succeeding generations are brought forth during the Summer, but they are wholly composed of females. In late Autumn, however, when the temperature begins to fall and food is scarce, the last generation produced contains both males and females, and the eggs of the latter are fertilized by the sperm of the former. These eggs remain dormant through the Winter and develop into females in the next Spring.

It has been shown experimentally that by maintaining the Summer temperature and the food supply artificially, the production of female generations among plant-lice can be rendered continuous through the Winter. It thus appears that parthenogenesis can in part be influenced by the physical environment.

We have seen that the maturation of the ovum consists in the throwing off of three-fourths of its chromatin, thus reducing the cell to the morphological equivalent of half a vegetative one, and that, before development can proceed, the egg must be raised to the value of a whole vegetative cell by the introduction of the chromatin of the male cell. It seems strange that the act of fertilization should return to the egg some portion of a substance similar to that which was thrown off during maturation, and we not unnaturally inquire, Whether there are not some eggs that in the process of maturation stop short of ejecting their chromatin at the first polar body, so that the egg retains the morphological value of a whole vegetative cell? And if we

find that there are some eggs that do thus stop short, the obvious question that we should ask would be, Do such cells, in virtue of the fact that they have the morphological value of a fertilized ovum in respect of the number of their chromosomes, develop at once and without fertilization? The answer is that, with but one or two questionable exceptions, all parthenogenetic eggs throw off only one polar body. It thus appears that, if the sexual cell retains the value of a vegetative one, it possesses the power of dividing and giving rise to a new organism without being fertilized by the male cell. But it also appears that in the immensely greater number of instances Nature has ordained that the individual shall possess a constitution, in more or less equal proportions, derived from a male and female parent; in other words, that an individual shall be the embodiment of two others. And in order to attain this end she reduces the morphological value of ova to such an extent that they cannot develop until their value has again been raised to the requisite extent, by the entry of the sperm [1].

It may be that such blending of the characters and physical properties of two individuals enhances the hardiness of the race and tends to its preservation, but it also may be that the phenomena have another significance. It will require very extended investigation before the meaning of these interesting facts can be said to be understood.

CHAPTER XXIII

HEREDITY

What is heredity? We often hear it spoken of as a 'force' or 'principle,' but it is neither. It is a name applied to the quality or property that is passed on from one generation to the next succeeding; a property by which the characteristic features of an organism, even in their minutest details, are transmitted to its progeny. The current generation of a race is related to the antecedent one in virtue of this property alone, which it has received from it, and it will be similarly related to the generation that it, in its turn, will beget; hence heredity may be further defined as the name applied to the relation that exists between successive generations.

[1] The student must not interpret this as meaning that Nature has intelligently or deliberately marshalled her forces for the attainment of sexuality. 'Natuie has ordained,' &c., is a mere figure of speech.

The ultimate cause of heredity is unknown; but the restless seeking for final causes that characterizes the intelligence of man has surrounded the few known facts with many hypotheses, which does credit to his ingenuity and fertile imagination, but which leaves the problem still unsolved. It is not, however, one of those problems that we must regard as unsolvable, but only very difficult of solution because of the great complexity of its factors. In every great question, that which leads quickest to a final, or approximately final, solution of the question is not an aimless searching for scattered facts, but the ascertainment of a definite order of facts in support of or opposition to a premise; if the premise be true it forms the basis for the formulation of another, which in its turn may be tested by an appeal to that particular combination of facts which will exist if it be true. And a hypothesis is of the nature of a premise; it forms a working basis from which an investigation may proceed, and by which its energies are prevented from being dissipated or weakened by following a path nowhither. If a premise be true the facts of the investigation will be capable of interpretation in harmony with its propositions, and, if such be the case, the premise becomes a finished portion of the road along which future investigation will proceed. If it be false, then obviously it is futile effort to pursue the inquiry along the direction which it indicates, and from the facts that proved its falsity the probable true direction may be indicated. And this is the true value of hypothesis in science; it stimulates the search for fact and circumscribes the field of investigation. It never becomes an infallible dogma, however eminent the authority whose intellect gave it birth; if inconsistent with the progress of knowledge it is rejected and replaced by another more in harmony with the present range of facts.

'Like begets like,' 'a chip of the old block,' 'what is bred in the bone will out in the flesh,' are popular conclusions in respect of human life, that the investigations of biologists have shown to be true of all forms of life. The resemblance between the parents and the offspring among the lower forms of life is not only physical, but is true also of their instincts; and with man is equally so of his physical, moral, and intellectual qualities. Culture can achieve something, in the case of man, in modifying the influences of heredity during the lifetime of the individual; such modifications, however, are not hereditary, for all refinements of manner, of speech, and of action must be reacquired in the offspring. The hereditary transmission of acquired characters is a much debated subject, and we shall return to it later.

Probably one of the first questions that would present itself to any one approaching the study of heredity for the first time would be, Does the male or female parent most influence the features of the offspring? Or, in other words, Does the offspring more often resemble the father than the mother, or vice versa? In endeavouring to arrive at a conclusion we must investigate the transmission of some character that is of a definite nature and capable of precise expression in language. It is to Galton, the great English authority on all questions relating to heredity, that we owe the collection and statistical treatment of a great mass of facts, and which has resulted in definite answers being given to many questions of heredity. Galton investigated the colours of foal offspring resulting from the crossing of definitely coloured sires with equally definitely coloured dams. His investigation was confined to all the possible combinations resulting from the crossing of four colours, i. e. chestnut, bay, brown, and black. From this combination of four colours chestnut dams may be crossed with bay, brown, and black sires, or bay dams may be crossed with chestnut, brown, and black sires; and similarly with the remaining colours. If the results are recorded we may note the percentage of foals which in colour resemble either their sire or their dam. The following table by Galton shows in a concise form the results obtained:—

Colour of the Dam.	Per cent. of offspring who in colour resemble their DAM.						Total.
	Sire.	p.c.	Sire.	p.c.	Sire.	p.c.	
Chestnut	Bay	33	Brown	0	Black	6	39
Bay . .	Chestnut	63	Brown	79	Black	60	202
Brown .	Chestnut	10	Bay	18	Black	38	66
Black .	Chestnut	30	Bay	24	Brown	33	87
							394

Colour of the Sire.	Per cent. of offspring who in colour resemble their SIRE.						Total.
	Dam.	p.c.	Dam.	p.c.	Dam.	p.c.	
Chestnut	Bay	30	Brown	16	Black	30	76
Bay . .	Chestnut	61	Brown	66	Black	53	180
Brown .	Chestnut	11	Bay	14	Black	50	75
Black .	Chestnut	3	Bay	7	Brown	40	50
							381

After Francis Galton. From *Nature*, vol. lvi. p. 598.

An examination of these tables shows that in one hundred cases where a chestnut dam was crossed with a bay sire, thirty-three of the resulting foals resembled the dam, and that, when in a similar number of cases a chestnut sire was crossed with a bay dam, thirty of the foals resembled the sire. In respect of these two colours it thus appears that the relative influence of the male and female in influencing the colour of the offspring is the same. It is markedly different, however, if we take another combination, such as the black dam with the chestnut sire, in which thirty per cent. of the foals are black in colour; but when reversed, with the chestnut dam crossed by the black sire, only three per cent. are black. In this case the influence of the dam is much the stronger. On the other hand, the influence of the male is the stronger in the combination of chestnut-brown. If however we consider the general result as indicated in the total, we find that the relative influence of male and female is much the same, i. e. as 394 : 381 = a difference of 0·7 % in favour of the female. Substantially, therefore, the potency of the sire in transmitting colour is the same as the dam. It is to be noted, however, that the bay colour is more highly prepotent than the others, since when the bay dams are crossed with sires of the other colours, and the bay sires are crossed with the dams of the other colours, the total of bay foals is very large in either case.

Another question of great interest is in respect of the relation of the sex of the progeny to the sex of the parents. Does the male progeny more often resemble the male or female parent? And similarly with respect to the female progeny. This question has been investigated in the case of horses by Howard Collins, who examined the offspring of 1566 mares of a special class and found the results were as follows:—

1566 {
- 707 {
  - 313 colts were of the same colour as the dam.
  - 394 colts were not of the same colour as the dam.
- 859 {
  - 373 fillies were of the same colour as the dam.
  - 486 fillies were not of the same colour as the dam.

Of the progeny of the mares investigated the fillies are more numerous than the colts, and hence, in seeking to ascertain whether the male or female progeny more frequently resemble the male or female parent, an allowance must be made for this; and when this has been done it will be seen that for every 102 fillies resembling their dam there will be 104 colts. On the other hand, when the same correction is made, it will be found that for every 131 colts of the same colour as their sire there will be 133 fillies. We may say, there-

fore, that the male and female progeny do not exhibit any marked tendency to resemble one parent more than another, but that the male progeny slightly tend to resemble their mother and the female their father.

Among animals and mankind no fact is more patent than that some individuals dominate, or are successful beyond their fellows in virtue of the possession of some remarkable characteristic; and the facts of heredity show that this dominancy of character or physical feature may be impressed upon the progeny through several successive generations. If a Highland heifer, which is a long-horned, light-coloured breed, be crossed with a Galloway bull, which belongs to a hornless, entirely black breed, the offspring is always a Galloway bull, indistinguishable, even to experts, from the pure breed. Hence the influence of the Galloway bull is so strong that its characters are impressed upon the offspring in such a predominant fashion that they are entirely like it. The same fact is demonstrated if we deal with horses, taking speed as the character for criterion, and allowing as the minimum speed entitling to distinction trotting or pacing a mile in 2′ 30″ or less. Galton investigated the offspring of 716 sires and 494 dams of American trotting horses, with a view to ascertaining the number of standard performers produced by each; reducing his results to percentages he formulated them in the following table:—

	Number of standard performers produced by a single parent, sire or dam.											Total parent
	1	2	3	4	5	6–10	11–20	21–30	31–40	41–50	50 and over.	
Sires	46	17	10	7	3	9	4	1	1	1	1	100
Dams	50	35	10	3	1	1	—	—	—	—	—	100

From *Nature*, vol. lviii. p. 247, after Francis Galton.

Thus out of the selected sires forty-six of them produced each only one standard performer, seventeen produced two, ten produced three, and so on for the remainder of the table. In the first five columns there is no indication of any marked prepotency (power of impressing personal characters upon offspring), for it must be remembered that a stallion can produce thirty foals annually and a mare only one, and that these results deal only with animals not less than twenty-five years old. So that, assuming all conditions to have been favourable, each sire represented in the table could have produced $(25-3) \times 30 = 660$

foals, and each mare twenty-two foals[1]. But in the last columns the prepotency of a few sires is very marked. In the list of 716 sires 460 of them were the foals of five distinguished sires, severally derived as follows:—

	Blue Bull	begot distinguished offspring			60
Sires by *Hambletonian* 10.	*Strathmore*	,,	,,	,,	71
	George Wilkes	,,	,,	,,	83
	Happy Medium	,,	,,	,,	92
	Electioneer	,,	,,	,,	154
					460

These figures show that certain individuals so impress their characteristics upon their progeny that, notwithstanding the fact that a particular sire has been crossed with different mares, the foals inherit the characteristic features of the sire. And this fact becomes still more demonstrable when it is ascertained that of the five distinguished sires the four most distinguished are the sons of one remarkable stallion, *Hambletonian* 10. *Hambletonian* has thus impressed his personal character of high speed upon two successive generations, and it will be a matter of great interest to ascertain, when the time comes (about 1921), through how many more generations he has impressed it.

Galton has frequently insisted that high prepotency is of the nature of a highly heritable sport or aberrant variation, and that it has probably played an important part in the evolution of races; that new races have arisen, not from small variations gradually accumulated through many generations, but relatively quite suddenly from highly prepotent animals. And he further states that, 'Certainly the successive improvements of breeds of domestic animals generally, as in those of horses in particular, usually make fresh starts from decided sports or aberrancies, and are by no means always developed slowly through the accumulation of minute and favourable variations during a long succession of generations.'

Francis Galton's Law of Ancestral Heredity.

It is a fact very commonly known that a child or an animal may resemble one of the grandparents, or one of a remoter ancestry, in virtue of some character not present in the parents, or, in the loose and vague language of popular usage, 'the child resembles the grandparents more than the parents.' Such a fact shows that the generation

[1] A horse may live for thirty or forty years, and it is sexually mature between three and four years of age.

of the ancestry beyond the parents contributes to the sum total of the physical and intellectual characters; and the question is, to how far back can this contribution be traced, and what is the proportion of the whole of the personal features contributed by each generation? Galton originally based his law on four general and *a priori* considerations, which he has stated in the following sentences: (1) Particulate germinal matter is necessarily limited in space, because in the ripening of the ovum and the sperm one-half of the germinal material contributed by each is lost. (2) The fact mentioned above that any remote ancestor may also contribute his peculiarity of feature or intellectual trait, and that independently of the rest. (3) The contribution of the two parents to the child is analogous to that contributed to the two parents by the four grandparents, and to that contributed to them by the eight great-grandparents, and so on, so that it is possible that the links of the chain of ancestral contributions form a geometric series of terms, diminishing as we proceed from the ancestor downwards. (4) The sum of the contributed heritages must be equal to 1.

The Law[1]. Thus it may be supposed that the two parents contribute between them $\frac{1}{2}$, the four grandparents $\frac{1}{4}$, the eight great-grandparents $\frac{1}{8}$, and the sixteen great-great-grandparents $\frac{1}{16}$. Or, that each parent contributes $\frac{1}{4}$, and each grandparent $\frac{1}{16}$, and so on. Hence, if N be the order of any given generation ($N = 1$ for parents, 2 for grandparents, 3 for great-grandparents, and so on), then $2^N =$ the number of ancestral places in the N^{th} order, and $\frac{1}{2}^N =$ the contribution of the N^{th} generation. And further, $\frac{1}{2}^{2.N} =$ the contribution of each ancestral place, i. e. the proportion contributed by *each individual* of the N^{th} order of generation. Hence $\frac{1}{2}^{(1)} =$ parents, $\frac{1}{2}^{(2)} =$ grandparents, $\frac{1}{2}^{(3)} =$ great-grandparents. Therefore the sixteen great-great-grand-parents are together no more efficient than a single grandparent, and only one-quarter as efficient as a single parent, for

$$(\tfrac{1}{2})^N = (\tfrac{1}{2})^4 = \tfrac{1}{16} = \text{the heritage of the 16 G. G. G-P;}$$
$$\text{and } (\tfrac{1}{2})^{N\times 2} = (\tfrac{1}{2})^{2\times 2} = \tfrac{1}{16} = \text{,, ,, a single G-P;}$$
$$\text{and } (\tfrac{1}{2})^{N\times 2} = (\tfrac{1}{2})^{2\times 1} = \tfrac{1}{4} = \text{,, ,, ,, ,, P;}$$
$$\text{and } \tfrac{1}{4} \div 4 = \tfrac{1}{16}.$$

The verification of Galton's theory is based upon the accordance which he obtained of the results of a series of calculations with

[1] The law is pictorially illustrated by an ingenious diagram published in *Nature*, vol. lvii. p. 293.

observed numbers. The requisite material for the purpose of the observations and calculations were obtained from the registered colours of a pedigree stock of basset hounds. The stock was started twenty-four years ago, by the purchase by Sir Everett Millais of ninety-three selected hounds, the most valuable descendants of which have been subsequently interbred. The pedigree of each animal has been kept, and contains a record of the name, parentage, date of birth, colour, and breeder. The result is a collection of 817 hounds of registered colours, &c., descended from parents whose colours are also known. Of these, in 567 cases, the colours of all four grandparents are known, and again of these, in 188 cases, the colours of all eight great-grandparents are known. Thus there are three sets of cases: (1) the known colour of the parents, (2) of the grandparents, and (3) of the great-grandparents. The records of these three sets were tabulated and discussed, and supplied the requisite material for comparing calculated results with observed ones. The statement of the actual calculation is of a complex nature, and the student desirous of further information may obtain it by reference to the original paper, read before the Royal Society on June 3, 1897, or to an extract published in *Nature*, vol. lvi. p. 235. The results of calculation, based upon known facts, correspond very closely with the facts derived from observation; in the second set the results of calculation were 391, that of observation 387, and in the third set as 180 to 181; this is a correspondence between the result of observation and that of calculation sufficiently close to prove the law.

Longevity. Is the capacity of living long lives heritable? Karl Pearson and Miss Mary Beeton have shown that directly and collaterally it is inherited in the male line; their investigation with respect to the female line is not yet completed.

Brachybioty. Brachybioty or short-livedness in respect of its heritable nature has not yet been investigated.

Telegony. There is a popular belief that, in the polygamous arrangements of animals, a foal of a dam may resemble not the current sire, but a previous one. It is stated by De Varigny that an ordinary tailed cat, which had kittens to a tailless Manx tom-cat, subsequently produced several tailless kittens when crossed with tailled toms of her own breed. This apparent harking back to a distant sire of another breed is called, in popular language, the 'infection of the germ'; and it is popularly thought that some of the unused sperm-cells of the Manx cat had lived for a greater or longer period in the oviduct of the

tailled cat, and had subsequently fertilized her ova at about the time that she was crossed with a tom-cat of her own breed. But Professor Ewart has shown that, in the case of horses, where apparent telegony also occurs, such a second fertilization by the same sperm is impossible, since the sperm of the sire has been proved not capable of living for a period as long as that occupied by gestation; and hence the death of the unused sperm of the first sire takes place before the birth of its foal, and therefore before the subsequent impregnation by another sire.

Professor Ewart has performed several experiments designed to prove or disprove the popular hypothesis of telegony. He has crossed many horse mares of different breeds with a zebra stallion, and subsequently crossed them with stallions of their own breed. But only in two cases did the foal of the stallion sire by the previously crossed zebra dam show any signs of a zebra-marking, and in all the remaining instances no signs whatever of zebra-markings were present. The two exceptional cases, which apparently support the hypothesis of telegony, can, however, be otherwise explained; for cases of zebra-marking upon the legs, sometimes even on the face, are known in cases of pure crossing, and where there has been no zebra connexion whatever. Devonshire and Welsh ponies not infrequently exhibit markings upon the fore-legs and the shoulders, and the common ass sometimes shows transverse bars upon the legs, like those upon a zebra, and sometimes the normal stripe upon the shoulder is double instead of single. The hemionus sometimes shows a shoulder-stripe, and generally it is also striped upon the legs. The quagga is very like the zebra, but is not striped upon the legs; but sometimes a quagga shows leg-markings. In the north-west part of India the Kattywar breed of horses is generally striped. Very often the foals of horses are striped, but the stripes quickly disappear before maturity is reached, and in those cases where the stripes persist throughout life, they are always more distinctly marked in the foal. The mule, derived from the crossing of the ass and the horse, is very apt to have its legs marked with zebra-like markings, though neither horse nor ass possessed them. Now the great feature of these markings is that they appear in the principal species of the horse genus, and, moreover, in species which are geographically widely separated. And Darwin's interpretation of this is that the ass, the hemionus, quagga, domestic horse, and zebra have all been derived from a common stock which was marked like a zebra, though it might have been different in other

features. The occasional appearance of zebra-markings in individuals of species normally unstriped is looked upon as a reversion to ancestral features, such as we should expect in the light of Galton's law of heredity.

We are therefore justified in regarding the two exceptions in Ewart's experiments as being cases of '**reversion**' to ancestral characters, rather than as proof of telegony. Such reversion is sometimes known as '**atavism**.'

Another experiment of Ewart's may be cited, as illustrating how easy it is to rush to a conclusion that a case of telegony has arisen, when as a matter of critical examination it can be shown not to be so, and that it may be more reasonably regarded as an instance of reversion. Ewart crossed a black West Highland mare, named Mulatto, with a zebra stallion; the foal, named Romulus, was born August, 1896, and on the whole was more a zebra than a pony, both mentally and physically. Romulus was more profusely marked than his sire, he had a semi-erect mane (zebras have an erect mane), in his movements he was, like his sire, alert and suspicious of unfamiliar objects. In his call he more resembled the sire than the dam, and the stripes were reddish-brown on the head and dark brown or black elsewhere. He was therefore remarkable in his unmistakable zebra-nature.

Now in July, 1897, Mulatto, the dam, was crossed with Benazrek, a high-caste, grey, Arab horse. The foal agreed in make, action, and temperament with ordinary horse foals, but differed in that it was *indistinctly* marked with a number of stripes, which varied from dark bay to brown. In such a case as this it might be easily urged, by persons not in the habit of critically examining their evidence—and it was from such that the idea of telegony first arose—that this was a case of resemblance to a previous sire, i. e. the zebra. But the markings, neither in number, distinctness, nor colour, are not those either of Romulus or the zebra sire; and if it were an instance of resemblance to a previous sire the markings ought to have been those of the sire.

In May, 1899, Mulatto had a third foal by a West Highland pony like herself, named Loch Corrie. The foal was striped like the second foal by the pure bred Arab, and differed as did that from the stripes of Romulus and the zebra sire. Since then (1899) two other West Highland mares, which we will call M^1 and M^2, have had foals by Loch Corrie. Now neither of these mares have ever seen a zebra, but their foals are indistinctly striped like the second and third foals of Mulatto. In the last three crossings, i. e. Mulatto, M^1, and M^2 with Loch Corrie

respectively, there is a common factor associated with the faintly striped offspring, and in M^1 and M^2 there is known to have been no zebra-crossing at all. It is therefore obvious that the markings in these two cases are not telegonic in nature, and that the only common factor is Loch Corrie, a West Highland stallion; hence the stripes in the foals of M^1 and M^2 are a reversion to long distant ancestral features induced through Loch Corrie. And if that is so, then Mulatto's third foal may be similarly explained, and since this foal was marked like the second, which was produced by the Arab crossing after the zebra sire, then that also may be similarly explained.

This apparent case of telegony, therefore, which would have met at once with popular acceptation, is, when critically examined by means of experimental facts derived from experiments deliberately designed to prove or disprove a given hypothesis, shown not to be so, because the markings were not what they should have been, and because the subsequent evidence, when examined in conjunction with previously known facts, can more satisfactorily interpret it as a case of reversion.

Telegony, like many other popular ideas, when stripped of its traditions and its venerable antiquity, and subjected to the test of accurate investigation, is found to have no foundation in fact.

Acquired Characters: Are they hereditarily transmitted? One of the modern questions of Biology around which there has centred a prolonged controversy is that of the transmissibility of acquired characters from the parent to the offspring. The idea of such a transmissibility was first put forward by Lamarck about 1795, in one of four laws, by which he endeavoured to explain the whole organization of animals and plants, in the following form:—'All which has been acquired or changed in the organization of animals in the course of their individual lives is conserved by generation, and transmitted to new individuals which proceed from those which have undergone those changes.' In other words, a character acquired in the course of the lifetime of the individual is transmitted through hereditary agencies to the offspring. For many years this hypothesis of Lamarck was accepted almost as an axiom, and even at the present time is strenuously upheld by a few biologists of repute. But in recent years the doctrine has been questioned and attacked by Weismann, Francis Galton, Ray Lankester, and others, and many of the arguments that used to be urged in its favour have not stood the test of investigation, and nearly all the remaining ones can be better explained by other means.

As in other complex controversies much irrelevant matter has been introduced, and in this case because there has been no exact definition of what is meant by 'acquired characters.' We may insist, with Weismann, that there is no such thing as an 'acquired character,' for 'an organism cannot acquire anything unless it already possesses the predisposition to acquire it,' 'for every acquired character is simply the reaction of the organism to a certain stimulus.' No one will deny that a predisposition to acquire this or that character may be hereditarily transmitted, but it is quite another matter to assert that a new character acquired in the life of the individual, and which was never present in its ancestry, can be reproduced in its progeny. And many of the facts upon which the doctrine has been supported have, when investigated, been shown to be devoid of the one essential proof, i.e. that the character which appeared in the offspring, and which was asserted to have made its *first* appearance in the parent, was in reality a new character; that is, the exponents of the doctrine have failed to show that it did *not* appear in the more or less remote ancestry, and that its appearance in the offspring is not simply a matter of reversion or the development of a latent character. This objection applies especially to arguments like that, for instance, urged by E. Roth, that in pathology the fact is everywhere evident that acquired local disease may be transmitted to the offspring as a *predisposition*. It is necessary to prove, as Weismann insists, that the causes which led to the particular predisposition are in reality acquired and not congenital; and this proof has not yet been forthcoming.

If by the term 'acquired character' we are to understand a structural or mental variation appearing for the first time in the life of the individual, then it is difficult to conceive how such a variation can be transmitted to the progeny. Because, as Francis Galton has urged, the ova of the mother are with her potentially before she is born, and with a little reservation the same is true of the sperm; and it is difficult to conceive that acquired characters can affect that which is already formed. And the plea that the embryo of a placental mammal may be affected by the admixture of the parent's blood with its blood is not tenable, because there is no such mixing of blood; the blood-vessels of the embryo have no connexion with those of the parent, and neither are the nerves of the one connected with the nerves or tissues of the other.

The fairest treatment of a disputed question is that which presents the principal arguments and facts of either side, and as far as possible

without bias; and I propose to present such facts and arguments for the affirmative side of the question as still retain some cogency, or are as yet unanswerable, and then to present the facts for the other side.

Among some of the arguments in favour of the hereditary transmissibility of acquired characters, that cannot be at present definitely dismissed, are those based upon the accumulated effects of the use and disuse of an organ. It is asserted that the bones of our common domestic duck weigh less than those of the wild breed, from which by domestication it has been evolved, and that the former has lost the power of continuous flight. It is contended that this is the result of the disuse of the wings through long generations; disuse of the organs of flight has produced partial degeneration of the muscles and bones, which has been accumulated and handed down through successive generations. It is urged that if the effect of the disuse of an organ is not hereditarily transmitted, then the domestic duck of to-day ought to fly as vigorously as the wild duck; and since it does not, then it follows that these effects have been transmitted. Such facts are, at first sight, apparently unanswerable, and in the present state of knowledge are in reality unanswerable. But before the argument can be accepted as final, it is yet to be shown that if the young of the domestic duck were, from the day of their hatching, associated with and reared by the wild breed, that they would still exhibit loss of the power of sustained flight. For, as Lloyd Morgan has shown, young birds soon acquire certain habits by imitation of those of their parents, and obviously, young ducks reared by older ones that do not attempt to fly, would likewise, by imitation, not attempt it. And it is a well-known fact that degeneration of an organ through disuse may easily result in the course of a single lifetime. Hence, the lesser weight of the bones of the arms, the lesser development of the alar muscles, and the loss of the power of sustained flight, may well be a matter of acquisition in the course of each individual life. It therefore needs to be shown, by the exponents of the affirmative side of the question, that if the freshly hatched ducklings of the domestic breed were reared by the wild duck, that the loss of flight still remains, and that the difference in the weight of the alar bones holds true of the young birds as well of the old ones. If this can be proved, then I think that their argument is final.

The kiwi, or flightless bird of New Zealand, possesses only the veriest vestiges of wings and has completely lost the power of flight. It lives on the ground among thickets and underwood, its chief food

consisting of insects and worms, in searching for which it is greatly assisted by its long beak and its delicate sense of touch. Now, why has the kiwi lost its wings? Was the loss of the wing the primary cause of its having forsaken an aërial mode of life for a terrestrial one? Or was the adoption of the terrestrial mode of life the cause of the loss of its wings? In the country where it lives it had few enemies, for the Mammalia were represented by two species only of bats, and the indigenous birds of prey are few. Hence, it had no need to fly, for it was safe upon the ground, and the food that it required was to be found there. It is argued that the kiwi is another instance of the hereditary transmission of the effects of disuse: here is a bird that once possessed wings, and could fly, but which, because of the absence of enemies on the ground and an abundance of food-stuff there, has given up flying altogether, and, as the result of the disuse of its wings through countless generations, has finally lost them completely. Weismann endeavours to explain these facts in another way, by a process which he calls 'a reversal of natural selection' or **panmixia.** **Natural selection** is that process of nature which comes into operation as soon as the number of individuals becomes greater than there is food material to supply. Under the conditions of the struggle for existence thus produced only those best fitted, in virtue of some congenital or innate structural variation, to survive will live and reproduce their species. The progeny of these structurally best-fitted individuals will inherit the variation that rendered their parents best fitted to survive, so that in the course of generations the unfit will be eliminated. Now Weismann argues that, as soon as any organ ceases to be useful to an animal, and no longer confers any advantage upon it not possessed by its fellows, natural selection will cease to operate, and it will make no difference in the struggle for existence whether the organism possesses this organ strongly or weakly developed. Under such conditions there will be sexual crossing of the individuals having weak and smaller wings with those having stronger and bigger wings; the progeny resulting will thus possess wings neither as strong or as big as the one parent, nor as weak or as small as the other, and in the course of several generations the result of indiscriminate sexual crossing of this kind will result in the production of a race with weak and smaller wings, and with a tendency to get weaker and smaller. Ultimately they will disappear altogether.

An organ which is never used is useless, and is an encumbrance; and in this particular case it would indeed be a distinct disadvantage to

the bird to possess wings, since a bird with this organ fully developed would be able less easily to escape through the undergrowth, and reach its hole in the ground, than would one with smaller wings, when pursued by one of the few indigenous birds of prey or by the aboriginal inhabitant. Hence, those members of the species which tend to vary in the direction of a reduction of the wings are better fitted to survive than those which show no such variation, so that the reduction of the wing will not only be brought about by panmixia, but will be hastened, when panmixia has produced a certain amount of retrogression, by natural selection once again operating. The disappearance of the wings of the kiwi can thus be explained without assuming the existence of a process for which no positive evidence has ever been adduced.

Professor Theodor Eimer, one of the principal German exponents of the hereditary transmission of acquired characters, argues that the black pigment developed in the skin of the African tribes of the tropical regions, due to the action of the intense light of those regions, has become hereditary, and that, therefore, this feature of blackness acquired under special conditions is transmitted from generation to generation. But it seems to me that in this instance, as in many others, the exponents of this doctrine have failed to distinguish between the action of a continuous environment and transmission from parent to offspring. For surely, if the intense light of the tropical sun produces blackness in the parent it must similarly produce it in the offspring, and, therefore, it is merely a question of the action of the same environment upon similar material. Moreover, if the black character has been acquired and is hereditarily transmitted, we should expect that it would be in evidence at the moment of birth; but such is not the case, for Eimer himself states: 'and the negresses (of tropical Africa) give birth to light-skinned children.' I do not assert that because the black colour does not appear at the moment of birth that it necessarily discountenances the idea of its hereditary transmission, but only that it leaves this example open to the other interpretation which I have placed upon it.

Several arguments based upon the instincts of animals have been adduced in favour of the affirmative side of the question, and one which appears less open to criticism than the others is this: Bees, as we know, collect honey from flowers during that period of the year when plants flower and the nectar is formed, and store it for use in Winter when the flowers are dead and nectar cannot be obtained.

This collecting and storing of honey is instinctive, for it is performed by successive generations without instruction from a preceding one, or without experience. But if bees are taken from a country where such conditions prevail, where periods favourable and unfavourable for collecting alternate, to countries, such as Australia, where honey can be collected the whole year round, the instinct of collecting a store for future use is said to disappear in a comparatively short time. In other words, bees possessing the hereditary and congenital instinct of collecting soon learn that collecting is a needless activity, and cease performing it; and this acquired instinct is hereditarily transmitted. If the facts are as stated certainly it is a strong argument in favour of the transmission of acquired characters.

Another line of argument is that derived from artificial mutilations or experiments. Brown-Séquard divided the sciatic nerve of two guinea-pigs, dam and sire of a litter; the result was muscular atrophy on the upper and lower sides of the thigh in either parent. The offspring of these guinea-pigs exhibited a similar atrophy in the same region of the thigh. At first consideration such experiment seems convincing, but it is open to the objection that we do not know the ultimate causation of muscular atrophy, and it may be that the section of the nerve is rather a secondary than a primary cause; and it has not yet been proved that the appearance of the muscular atrophy in the offspring was not acquired by infection or otherwise in their own lifetime. In support of these objections, another experiment of Brown-Séquard may be mentioned. He divided the cervical sympathetic nerve of two rabbits, buck and doe, as the result of which a permanent drooping of the upper eyelid was produced; and this drooping of the upper eyelid was said to be inherited in the young. Leonard Hill subsequently repeated the experiments in six guinea-pigs, but took aseptic precautions to prevent inflammation of any part of the eye; the result was that none of the offspring exhibited any drooping at all. He then divided the nerve in twelve of the offspring, and interbred them; but no permanent droop ensued. A temporary droop was sometimes observed, but it was due to inflammation of the conjunctiva of the eye, and disappeared as soon as the inflammation was cured. Thus the apparent transmission of an acquired character was due to disease in the offspring, and was not hereditary transmission at all. And it is possible that all experiments of this kind may be explained in a somewhat similar manner.

Another argument used by the exponents of the affirmative side is

that derived from the blindness of cave animals and burrowing or underground forms. The common mole, for instance, is blind, for the eyelids are permanently closed, and the optic nerve early atrophies along a portion of its course. A burrowing rodent more subterranean in its habits than the mole, *Ctenomys*, or the Tuco-tuco, is also blind. It has been urged in the case of cave animals, that having become inhabitants of caves, either voluntarily or by some accidental cause, such as being washed in by streams, that in the absence of light eyes were useless, and were consequently never used. As a result, it is said that they degenerated, just as a muscle will degenerate if never used, and that the eyes ceasing to function through many generations, and the degeneration of them in each generation having been accumulated, ultimately there is produced complete blindness, and more or less reduction in size or disappearance of parts of the eye. Or, in other words, the eyes of the first generation atrophy to a certain extent, and the next generation are consequently born with weaker eyes, which atrophy to a still greater extent, and so on for succeeding generations. For it is urged that unless the effects produced in each individual life are inherited, and accumulate with each generation, how can a perfectly blind form, with atrophied optic nerve, arise from a form which originally possessed a perfect visual organ? Well, there are at least three other possible explanations. Darwin once kept a *Ctenomys*, which was certainly blind. On dissection, however, the blindness was seen to be due to inflammation of the nictitating membrane. Now it is almost certain that under the abnormal conditions that exist underground, inflammation of some part of the eyes must be of constant occurrence, and Darwin argues that as frequent inflammation must be harmful to an animal, and as eyes are not necessary to subterranean creatures, that blindness would be an advantage, and that natural selection would operate to preserve the blind and eliminate the blindless forms; that among the original stock that became subterranean, there would be some (a few would be sufficient) that possessed an innate tendency to become blind under favourable conditions, while others possessed no such tendency. Under the favourable conditions produced by subterranean life, those with the tendency to become permanently blind under some exciting cause, such as inflammation of some part of the eye, would possess an advantage over those which did not; and the offspring derived from two parents with such a tendency would have it intensified, and the offspring from any two of these which may

have interbred would have it still more intensified. Ultimately completely blind forms would result, and these would be more advantageously placed than those forms which, having no tendency to become blind, were repeatedly suffering from inflammation of the eyes, or from a chronic condition of that disease.

The other explanation of the presence of blind forms in caves and subterranean burrows is that of Professor Ray Lankester: 'The facts are fully explained by the theory of natural selection acting on congenital fortuitous variations. Many animals are born with distorted or defective eyes, whose parents have not had their eyes submitted to any peculiar conditions. Supposing a number of some species of Arthropods or fish to be swept into a cavern, those individuals with perfect eyes would follow the glimmer of light and eventually escape to the outer air, leaving behind those with imperfect eyes to breed in the dark place. In every succeeding generation this would be the case, and even those with weak but still seeing eyes would in the course of time escape, until only a pure race of eyeless or blind animals would be left in the cavern.'

The third explanation is that of **panmixia**, and is due to Weismann. He argues as follows: 'Now suppose such a species (newts capable of seeing) to have been carried underground by water into a dark cavern. It would only gradually adapt itself to the new conditions and thus be enabled to thrive in the cave; but after the lapse of generations the individuals would have learnt to live in complete darkness, and to distinguish and catch their prey without the aid of sight, and this would be rendered possible by an improvement in other organs, especially those of touch and smell. Thus in course of time a race of newts would be produced perfectly adapted for life in the dark, and for finding food by scent alone and not by sight; and this race would make its way farther and farther underground, and pass its whole life in utter darkness. Directly, however, such cave-dwellers became able to exist without using their eyes, degeneration of these organs would set in: as soon as they ceased to be essential to the life of the animal, natural selection would be powerless to affect them, for it would be immaterial whether the eyes of any animal were above or below the standard. Hence the individuals with weaker sight would no longer be eliminated, but would have an equal chance of surviving and propagating their species. Sexual crossing would then take place between individuals with strong and weak eyes, and the result would be a gradual deterioration of the organ, the process being very slow at first but absolutely sure.'

The student who desires further statements and facts supporting the affirmative side of the question will do well to study Eimer's book on 'Organic Evolution,' of which there is an English translation by Cunningham.

The negative side of the question is supported by many incontestable facts which cannot be explained in terms of hereditary transmission. With regard to mutilations, the loss of a finger, toe, or tail is not inherited. Certain races of mankind have practised for thousands of generations the rite of circumcision, and the aboriginal Australians a similar one; but in neither of these races have the effects of the mutilations been inherited, for the operation is repeated in every successive generation. The personal acquirements of the human race are not transmitted; for countless generations we have been able to read, to work out algebraical and arithmetical problems, to walk and to speak. But no child has yet been born who could read, calculate, walk, or speak, without first acquiring the art by laborious effort. In fact, so little has speech become an innate part of our organization that there are well-authenticated cases on record, according to Weismann, of young and adult persons found living in an utterly wild state in the woods of Germany, France, England, and Russia, who could not speak any human language, but only utter sounds that were imitations of the cries of the wild animals with which they had associated.

For generations oak-leaves have been pierced by gall-producing insects, but there is no evidence to show that galls arise on these or any other leaves without first being pierced by the insect.

For generations horses have been trained by trainers to acquire high speed, but such horses do not beget a progeny of fast foals more than untrained horses do. According to Francis Galton, A. J. Meston, from the study of careful statistical data, came to the conclusion 'that some trained stallions and mares had got foals that made fast records, but that the evidence did not justify the conclusion that a line of trained ancestors is more successful in producing speed than a line of untrained ancestors or a line of mixed trained and untrained ancestors. The evidence is thus negative that the capacity for speed, acquired by habit, training, or experience, is hereditary.'

Hereditary Instinct.

We have seen to what extent certain concrete characters are heritable, and we shall now consider a few instances of that more abstract quality of instinct. And here we must distinguish between instinct

and intelligence: instinctive acts are those performed without previous knowledge or experience, and intelligent acts are those which are adapted according to circumstances, and modified in virtue of acquired experience. The boundary line between these two kinds of acts is nowhere definite, and it is often difficult, if not impossible, to say of a given act that it is intelligent or instinctive.

We will now consider as to how far purely instinctive acts are hereditarily transmitted from parent to offspring. In a state of nature, the callow young of jackdaws, jays, and thrushes instinctively open their beaks for food to be thrust into their mouths by the parents. Even before their eyes are opened, and therefore before visual experience can begin, their mouths gape for food, and according to Lloyd Morgan, to whose researches we owe most of our knowledge of the subject, the external stimulus seems to be a shaking of the nest or a sound emitted by the parent bird. Professor Lloyd Morgan has subjected these callow young to experimental conditions; that is, he has hatched them in the absence of the parent birds, in order to demonstrate that all the actions which they commit are really instinctive, and are not acquired by imitation of those of the parents. And he has found that under these conditions a low whistle, click of the tongue, tapping of the box, or a lip sound, will set the young ones gaping. Thus the response of the young to certain external stimuli is hereditary, for they have under such conditions of rearing no chance of acquiring experience.

Under similar experimental conditions, fresh-hatched chicks will peck with more or less precision at grains of food put before them. And at first they will peck at anything, whether good or bad, until experience has taught them which to avoid and which to accept; thus if a young chick be given pieces of orange-peel it will peck at them, but the moment it tastes the flavour it will drop the piece at which it pecked, and will not touch any others for some time. And if this act be repeated many times, it will at last indefinitely refuse to peck at anything and will starve. Hereditary instinctive acts are thus soon modified by experience, and we then speak of them as being intelligent; this illustrates how confluent is the boundary between the two kinds of acts, for the one may become the other. The young moorhen, when fed in nature by the parent, is fed from above, while it floats on the water. When reared without parents it will readily take food held above it, but cannot be easily induced to pick it up from beneath.

The foregoing are instances of hereditary instinctive acts which result from two stimuli—internal hunger, and external sensory impressions.

A very beautiful and somewhat complex instance of hereditary instinct is that of the Yucca moth. The Yucca flower (flower of the plant known popularly as 'Adam's Needle') opens but for a single night, and the Yucca moth emerges from its chrysalis at the same time. Immediately it is liberated it begins to collect pollen from one flower, rolls it into a pellet, and then flies with it to the pistil of another. It then pierces the wall of the ovary and deposits its eggs within the cavity and among the ovules. Then it deposits the pellet of pollen upon the stigma of the pistil. It is proved that unless the stigma be pollinated by the moth, that the ovules will not develop; and unless they develop, the larvæ of the moth derived from its deposited eggs would starve. Now the insect performs all these acts immediately that it leaves the chrysalis, that is, as soon as it comes into existence; it can, therefore, have had no experience, can have gained no knowledge of what would befall its larvæ if not deposited in this exact position, or if so deposited what would be their fate if the ovules did not develop, neither can it have acquired any knowledge as to what is necessary in order that the ovules may develop; and yet unerringly, without guidance of any kind, not even of that which shall tell it which of the multitude of plants around it is the Yucca plant, it performs the one and only series of acts of its life, in proper sequence and without loss of time. Truly the possession of a valuable and orderly instinct is a better gift than that of a muddled intellect.

With birds, the acts of walking, swimming, and flying are hereditary instinctive ones. If chicks are hatched under experimental conditions (in the absence of parents), they can walk immediately on liberation from the shell; there is no elaborate process of learning. Ducks and moorhens, under the same conditions, swim with ease a few hours after hatching, when placed in water for the first time. Young swallows fly short and guided flights when committed to the air.

If such acts as walking are hereditarily instinctive, and if, moreover, as we believe, acquired characters are not hereditarily transmitted, then we should expect that in the young of a species that has undergone a change in its mode of progression in the course of its evolution, that the first and early efforts of progression would be not those of the species, but those of the ancestral stock whence the species arose. The structural facts relating to man and apes leave little

room for doubting that they have arisen from a common ancestry, and if this conception of man's origin is true, then his ancestry walked on all fours, and were more or less bough-grasping in their habits. Now so far as instinctive acts are concerned, it is to just such a conclusion as this that the behaviour of the human baby lends support; for the hereditary mode of progression of human babies is not the bipedal gait but the quadrupedal. In civilized races it is usually a pseudo-quadrupedal gait, not a true one, for the infant crawls on its knees and hands; but in uncivilized races it is a true quadrupedal mode, for the infant progresses on its hands and feet (not knees). But doubtless this difference is accidental, and is due to the mode of clothing adopted by civilized races, for in some instances, when the child is divested of its superfluous clothes, it will assume the true quadrupedal gait. The influence of this ancestral gait is very strong, and as Mr. S. S. Buckman points out in *Nature*, vol. lxii. No. 1601, p. 226, 'the child has really to unlearn it, and to readapt its hind limbs before it can attain the bipedal method of progression.' A child just learning to walk cannot keep its legs straight, for they are considerably bent at the knees; now such a bending is not consistent with the mechanics of bipedal progression, but it is with that of a quadrupedal progression, as may be seen by any one who will watch an infant or a monkey walking on all fours.

As Mr. Buckman points out, there is also another feature noticeable in the efforts of a child first learning to walk; it is the outspread position of the arms and the semi-clasped condition of the hands. Now this is a naturally, as it is an instinctively, assumed position, because our ancestors were bough-grasping animals. How much this semi-clasped position of the hands is part and parcel of the child's movements may be illustrated by watching it grasp any article. Mr. Buckman, in the article already referred to, gives a picture reproduced from a photograph, showing a child picking up a flower-pot and raising it towards its mouth. It does not grasp it in the way an adult would, between the index-finger and the thumb, but in the way that a bough-grasping animal would grasp a bough, by grasping its edge between all the fingers and the palm of the hand, the thumb not being used at all. And, moreover, in raising it to its mouth, it raises the other arm, with the fingers clasped upon the palm of the hand, in sympathy with the movement of the arm and hand that is grasping and raising the tangible object. In fact, so strong is this ancestral influence, that the infant cannot even grasp with one hand, but that

the instinctive response to such a stimulus simulates the similar response of a long-past ancestry, when not a flower-pot or other miscellaneous object, but the boughs of trees among which they lived, excited the internal train of nerve changes, that manifested itself in the closing of the fingers upon them. This ancestral influence extends far into life, even beyond infancy, into childhood; for if a number of school-children be asked to hold out their hands, the majority will not extend them flat, but will show a marked tendency to curve the fingers inwards, and it will be more pronounced in the younger than in the older children. The intense love of climbing exhibited by the average boy, and also the girl when not debarred by foolish ideas of propriety, is exceedingly suggestive, and must be regarded as a hereditary instinct.

Deferred Instincts. By deferred instincts is understood those which do not appear until some time after birth, and then they are in some measure modified by experience. The chick does not begin to scratch the ground until some four or five days after hatching, nor does the moorhen flick its tail until it is about four weeks old.

The knowledge of good or evil, in regard to matters of food or dangerous enemies, does not appear to be hereditary, for a chick will peck at anything until experience has taught it which is good and which is bad. The caterpillars of the Cinnabar moth are marked by conspicuous alternating bands of yellow and black, and have a repugnant flavour for most birds. In some experiments conducted by Professor Lloyd Morgan these were given to some chicks as food; they seized them, but immediately dropped them and wiped their bills. Later in the day they were again offered the caterpillars, but most of the chicks refused them, and some tried them but once. The following day some edible caterpillars were given, which were duly devoured by the chicks, and these were followed by the offer of some Cinnabar moths; but none touched them, though one chick ran towards one, but checked itself and wiped its bill. The memory of the obnoxious taste associated with yellow and black bands was recalled, and its instinctive pecking act was checked by its experience. Until experience has taught them the difference, young chicks will seize bees and wasps with neither more nor less fear than harmless flies and palatable insects.

The instinct of fear appears to be an acquired one rather than a hereditary one, for pheasants, partridges, and chicks show no signs of fear when a dog enters their shed, and when allowed to come to close

quarters, they peck at its legs; even more, a two-day chick tried to nestle under a dog allowed to come to close quarters and sit down. A fox-terrier once invaded the meal of sopped bread of a little moorhen and the latter fearlessly attacked him. A chick is perfectly indifferent to a cat until it has seen one swoop down upon one of the brood.

Nevertheless, they appear to evince fear of anything large or unfamiliar, especially if moved quickly or if accompanied with an unusual sound. Young pheasants and moorhens are struck motionless, and some scatter in all directions, at the sound of a chord struck violently on the violin. And a case is described of hereditary fear being evinced by a baby orang-utan when shown the fur of an Indian flying squirrel, under circumstances in which previous knowledge could not have been acquired.

Some Theories of Heredity.

Man is not satisfied with isolated facts; he strives to obtain a broad conception of their meaning, and to discern the general trend which they seem to follow. Ever since the time of Democritus, Paracelsus, and Hippocrates, theories which endeavoured to explain the why and wherefore of heredity have been propounded. There is a general family likeness among them all, and even in some modern theories one can still see the reflection of the ancient image. In 1864 Herbert Spencer propounded what may be called the first scientific theory, because it was based on a somewhat large range of facts, and which, if it did not explain them all, was not negatived by any of them. He suggested that minute particles, which he called 'physiological units,' were accumulated in the reproductive elements from all parts of the body, and there developed the characters of the cells whence they were derived. Four years later Darwin produced his 'provisional hypothesis of pangenesis,' in which he suggested that every cell in the body, which was not too highly specialized, budded off 'gemmules' which multiplied by means of fission and retained the qualities of the cells from which they were derived. These ultimately found their way to the reproductive organs, where they were organized into the sexual cells. In development the various gemmules grew into cells like those from which they originally came.

The fundamental feature of these two theories is that they regard the sexual cells as being aggregates of units or gemmules derived from

all parts of the body; now if such theories are true there ought to be no difficulty in recognizing the hereditary transmissibility of acquired characters, and, as we have seen, there is considerable doubt as to whether such transmission exists at all. And the distinct tendency of all the more modern theories, dating from Francis Galton in 1872, is that there is an unbroken continuity from one generation to another, and that the characters acquired from the parents by the offspring are such as were acquired by them at the same time that the parents acquired theirs; in other words, the child is, in a sense, as old as the parent. Galton granted that the ovum may be composed of a sum of 'physiological units,' 'gemmules,' &c., or of some units of some kind, but he maintained that these were not derived from all parts of the body of the parent, but from the ovum of the grandparent; and that when the ovum developed, the major portion of the units were organized into the tissues of the body, while a portion remained unaffected by the changes of development, and formed the sexual cells of the offspring. Thus in a sense the sexual cells are in the direct line of descent, the body being a mere lateral offspring. This idea of **organic continuity** is the basis of all modern theories of heredity, and the student would do well to try and understand it. Let us suppose that the ovum is composed of gemmules or units of some kinds, representing all the groups of cells (tissues) of which the adult individual body of any species is composed; we may call these different units 1, 2, 3, 4, 5, 6, 7, and 8. As development proceeds these units divide repeatedly, and the resulting products group themselves according to their different characters; thus specialization into this or that tissue proceeds, and the units become grouped into groups consisting of 1 and 2, 3 and 4, 5 and 6, 7 and 8, or other combination, and so on. But some of the cells derived from one part of the original do not specialize, and retain their characters of 1, 2, 3, 4, 5, 6, 7, and 8 unaltered; this part constitutes the sexual cells of the offspring. Thus the sexual cell of the offspring is the direct product of that of the parent, and so on backwards to the remotest ancestor, even to the common origin of all living things.

Thus each succeeding generation is organically continuous with its predecessor.

Such a theory may be briefly stated to be one which asserts that a certain portion of the original, undifferentiated, reproductive protoplasm of the ovum is set aside for the formation of the reproductive cells of the offspring, while the remainder becomes the body cells.

Now such a setting aside of a portion of the undifferentiated ovum has been observed in leeches, in *Sagitta*, threadworms, Polyzoa, *Chironomus* (an insect), *Moina* (a crustacean), and in certain spiders. In these animals, at the first or in some very early division of the ovum, one part remains unaltered and becomes the sexual cells of the developing organism.

De Vries and Hertwig followed later with slightly modified theories of pangenesis, but the most elaborate and latest is that of Weismann. It is too complex to deal with fully in these pages, but the student desirous of knowing the full nature of the theory, as well as the facts upon which it rests, may find them in two volumes of essays on 'Heredity,' by Weismann, of which there is an English translation in both cases. But we may give a brief outline of his theory. He regards the ovum as being composed of many particles or pieces called **ids**. Each id he regards as a regularly constituted colony composed of smaller pieces called **determinants**, conforming to a definite architecture, and occupying a definite position corresponding relatively to that occupied by the tissues of the adult. The histological character of every cell is determined by one determinant, and since the determinants can divide, one determinant suffices for every group of adult cells having different characters. Each ovum must therefore contain a number of determinants equal to the number of the different kinds of tissues of which the body of the adult is composed. Each determinant in its turn consists of other particles called **biophores**, which govern the assimilation, metabolism, and the power of reproduction by fission of each cell. The ovum must therefore contain a number of biophores equal to the number of the different kinds of cells which the adult body contains. Weismann supposes that when this complex ovum divides the first time it divides into two equal portions, each of which are alike. Of these two parts, one grows and divides repeatedly and forms the reproductive cells, and each succeeding division divides each part into two identical parts, for each contains the same kinds of ids, determinants, and biophores. Weismann speaks of this kind of division as an 'erbgleiche Theilung,' for which the English equivalent a 'doubling division' has been suggested by Dr. P. Chalmers Mitchell. The other of the two parts also divides, but each part resulting from the division is different, and this is called 'erbungleiche Theilung,' or its English equivalent, 'differentiating division[1].' Each division does not double the number of pieces, but sorts them out and rearranges them, placing

[1] Also suggested by Dr. P. Chalmers Mitchell.

one set of determinants in one portion and another in another. Thus suppose, for illustration, that this second part contains a certain number of ids, the first division would result in each part containing only one-half the number, and so on through a large number of divisions. A decrease in the total number of ids in each cell necessarily involves a decrease in the number of original determinants and biophores; and with each division the ids become less complex, that is, they contain fewer determinants; and ultimately each cell-group will contain only one determinant, which by division will produce one for each cell of the group. Each determinant will of course contain its appropriate biophores.

Thus Weismann's theory is essentially one of **organic or germ-plasm continuity**, and, so far as that goes, it constitutes no advance on that of Francis Galton. But it is more complex, because he endeavours to explain nearly every known fact of heredity, and to satisfy the details of embryological development. To a large extent he has succeeded, but it must not be forgotten that his theory is not open to attack on all sides, for it is partly based on assumptions which from their very nature cannot be disproved by a direct appeal to fact.

CHAPTER XXIV

VARIATION

THE facts of heredity show us that all organisms tend to beget their like, which are similar to but not identical with them. The progeny of nearly every individual organism differs in some smaller or greater feature from its parent, and to this tendency to differ the name of variation is given. The variation of a character or an organ may be very small and scarcely perceptible, or it may be very obvious and remarkable, and give rise to what is called a **monstrosity**. It may affect the organism with regard to the symmetry and number of its parts, when it is called **meristic variation**, or may affect the nature and quality of its substance, when it is called **substantive variation**. Either of these kinds of variation may be **continuous** or **discontinuous**. When the extreme forms of variation in a character are connected with the so-called normal form by variations which form a graduated series, we may speak of it as being a continuous variation (Fig. 99), and when there are big gaps or falls in the series, as a discontinuous variation (Fig. 100). The subject however is more complex

than such a statement implies, and it is doubtful whether any formal statement of this sort can accurately define the meaning of continuous or discontinuous variation; the student must therefore bear this caution in mind, and trust more to the facts than to the definition.

Let us consider some instances of meristic variation. The normal dental formula of the orang-utan (*Simia satyrus*) is

$$\text{i.}\ \frac{2}{2},\ \text{c.}\ \frac{1}{1},\ \text{p.m.}\ \frac{2}{2},\ \text{m.}\ \frac{3}{3};$$

but occasionally individuals appear in which there are a greater number of teeth than normal; for instance, a case is known of one where there is a fourth molar on either side in the upper jaw, and on the left side only in the lower jaw. Others are known in which an additional molar (m. 4) is present on either side of the lower jaw alone. In one remarkable specimen the upper right third molar was absent, and also the nasal bones of the face. In the dog numerous variations are recorded of the teeth: there are two known cases in which one of the incisors is absent; in one case the two inner incisors (i. 1), and in the other the two outer ones (i. 3). In several other cases supernumerary teeth are known, there being four incisors instead of the normal number of three. Supernumerary premolars and molars are also known, as well as a reduction in their number. These variations occur in wild and domestic dogs alike.

In man, increase or decrease in the number of the digits of the hand or foot is not an altogether rare phenomenon, nor is an increase in the number of phalanges of a particular digit. Normally the thumb of man contains two phalanges, but cases are known where it has three phalanges; others have also been described where, internally to the abnormal thumb, is an extra digit of two phalanges, and in other instances this supernumerary digit itself has three phalanges. There is also a condition known as 'double-hand,' in which the hand consists of two sets of digits arising from a single palm (middle-hand). In some of these each set of digits consists of four, each digit possessing three phalanges, and each set constituting the optical image of the other. In other instances there is a total of six digits, three in each set. Again, there are cases with a total of seven digits, consisting of an external group of four and an internal group of three. In some instances the variations of the digits are accompanied by variations of the wrist-bones and the bones of the fore-arm. In other instances the right hand is different to the left, neither being normal. Feet also show variations, in some of which the big toe (hallux) is very broad

and the phalangeal bones appear to be double, and on its inner side two supernumerary toes are present. In another case eight toes are present on either foot. Variations of a like nature occur in apes and monkeys also.

The condition resulting from an increase in the number of digits may be called **polydactylism** ; the reverse condition, i. e. that of a decrease in the number of digits by the fusion of certain of them, may be called **syndaetylism.** A few instances of this latter condition will now be considered. All grades of union exist, between a mere webbing of two digits together, through a condition in which the fleshy parts are fused, to a union of the bones ; the extreme and highest condition must be regarded as that where two digits are represented by a single one which is broader than the others, and can be looked upon as a kind of intersusception of two fingers within each other. Toes as well as fingers exhibit syndactylism. Certain features of this phenomenon seem suggestive; for instance, in the hand it is digits III and IV which most frequently fuse ; union between digits I and II is known in only one case, and between II and III and IV and V in only a few instances. In the foot, on the other hand, the most frequent cases of fusion are between digits II and III, that is between the index and the medius. In cases where the bones are involved in the fusion they are always most completely fused at their periphery (extremity), and less completely centrally (end near the middle-hand). Another feature of importance is the fact that the union is nearly always one of optical images. Let the student examine his hand, and for the moment disregard his thumb ; if he will imagine that the third and fourth digit were to become united along their opposed surfaces, then the plane of union would be one in which the two fingers on either side would form the optical image of the other, or nearly so.

Variations in the form of polydactylism and syndactylism are known among other Vertebrata besides man ; there are numerous recorded cases among the horse, calf, roebuck, sheep, heifer, deer, pig, ox, and various birds.

Ectrodactylism, or absence of digits in man and other animals, is known. It may be represented by the absence of only one digit, or by as many as four, so that only one digit remains.

Numerical variations in the number of the parts of organs of animals, such as antennæ and other jointed appendages of the Arthropoda, are of almost constant occurrence, as may be confirmed by any student who takes the trouble to examine a large number of crayfish or cock-

roaches. In the crayfish an instance is known of the first ambulatory appendage (great chela) bearing three pairs of chelæ. Of these one pair were the normal ones; of another pair each claw was the optical image (right and left) of the other; and the remaining pair were much smaller than the others. In lobsters and crabs instances are known in which the dactylopodite of the great chela bears an extra dactylopodite, the normal one being so prolonged and formed on its outer surface as to form with the extra one a biting surface, much as the propodite of a normal appendage does with its dactylopodite. Other instances of double appendages are known among Crustacea and also among Insecta.

The inheritance of variations of the kind just considered appears to be of frequent occurrence, and may be repeated in each generation for several successive periods. In some cases (polydactyle cats and an ox) the descent was wholly through the female line. Usually the inheritance takes the same form in the offspring as in the parent, but occasionally the variation, though affecting the same organ (such as a digit), may assume a different form; for instance, that which may be a case of duplicity of thumbs in the paternal grandmother may be, in the father and children, a thumb of the three-phalanged form.

Digital variation is in some cases associated with other forms of abnormality; polydactylism may be associated with hare-lip, defective dentition, defect of tibia, &c., and syndactylism with deformity and arrested development. At present there is nothing to indicate that there is any definite relation between these several variations, and further observations are much needed.

In goldfish the tail is not infrequently double, each being the optical image of the other, and only united a little way behind their common origin from the body. At the present moment such a case may be seen in the Fish-house at the Zoological Gardens in London.

Flat-fish (plaice, soles, turbot, halibut, &c.) are normally coloured on their upper and white on their under sides. Variations from this normal condition occur in one of two ways: the upper side may be colourless like the lower, or the lower may become pigmented like the upper. The pigmentation of the upper surface is rarely of a uniform nature, but is ornamented by spots or patches, more or less extensive and variously arranged in the different species. In the cases of variation where the normally colourless under side becomes pigmented, the resemblance is so close that the spots or patches on the one side occupy almost the identical positions of those on the other. In other words, the one side tends to become the optical image of the other.

The number of vertebræ present in the vertebral column of an animal is constant for the species, but occasionally the total of the number may be increased by the addition of one or more vertebræ. Man normally possesses four vertebræ in the caudal (tail) region, but instances are known where five are developed. Now and then vertebræ are observed which appear to be two adjacent ones partially fused together, or to be a single one imperfectly split into two. Such cases are known in various snakes and other reptiles, and in man; and a somewhat similar case is known in a rabbit. One instance is described of a rabbit's backbone, in which only one-half of the centra of the eighth and ninth thoracic vertebræ are represented, and in which the left half of the eighth is confluent in an oblique manner with the right half of the ninth. Another instance of variation in a rabbit's backbone relates to the twelfth thoracic of a young rabbit, in which the centrum consists of two pieces, situated right and left of the middle line, and the zygopophyses of either side are obliquely disposed. It is of such a nature that it could be interpreted either as the two halves of two adjacent vertebræ that are confluent in an oblique manner, like that of the one previously mentioned, or as one where the centrum has ossified from two centres. Neither interpretation, however, satisfies all the facts of this remarkable variation.

Homœotic Variation in Ribs and Vertebræ. By homœotic variation is meant the assumption by a vertebra of one series of the characters of that of another. We have already seen that the spinal column in Mammalia is divisible into cervical, thoracic (dorsal of human anatomists), lumbar, sacral, and caudal. The cervical region bears no movable ribs, and the vestiges of ribs which it possesses are firmly ankylosed with the centra and neural arches of the vertebræ; the thoracic region bears freely movable ribs, the lumbar region behind it does not; the sacral vertebræ are fused together and support the pelvis; and the caudal vertebræ are those lying behind the sacral, and are more or less vestigial posteriorly. Variations may occur in the different regions of the vertebral column which have no effect in reducing or increasing the total number of vertebræ, and these are those in which the vertebræ of one region may simulate those of another. But it is always the vertebræ of one region that assume the characters of the region next to it, not those of the region next but one; for instance, a cervical vertebra never resembles a lumbar vertebra, or vice versa, but always a thoracic one. And it is always the adjacent vertebra or vertebræ to the

region which it simulates that vary; for instance, in the cervical vertebræ it is the sixth or seventh, not the fourth or fifth which exhibit variation. In man the presence of ribs on the last (seventh) cervical vertebra is a relatively common incident, and they are sometimes fixed and sometimes freely movable. Cases of development of ribs on the sixth vertebra are extremely rare, and then they are very vestigial. Cervical ribs may be of all stages of development, from a mere stump to a perfect one connected to the sternum. The thoracic ribs sometimes are vestigial, in which case the homœosis is from the thoracic to the cervical type; in these instances the whole of the cervical vertebræ must be present, otherwise it is impossible to be certain that the case is not one of the development of a cervical rib. Frequently in man the last rib tends to retrogress and become smaller, in respect of which the last thoracic vertebra may be said to tend to resemble a lumbar one. Less frequently the first lumbar vertebra develops a small and imperfect rib. The last lumbar vertebra may unite with the first sacral, either symmetrically or unilaterally; or the first sacral may detach itself from the sacrum (fused sacral vertebræ) and become one of the lumbar series, and sometimes, though not necessarily, in this event the first caudal vertebra becomes confluent with the last sacral.

Not infrequently variation in one region of the vertebral column is accompanied by a correlated one in another part. For instance, if the last cervical develops a pair of ribs the last thoracic vertebra with its ribs disappears. There thus results a loss of one vertebra from the column as a whole. In this case one vertebra of a forward region simulates the characters of a region behind it; this is called **backward homœosis**, and whenever a variation in the total number of vertebræ accompanies it, it is always a reduction of the number. On the other hand, in **forward homœosis** any variation in the number of the total vertebræ is always an increase in the total. This kind of homœosis is illustrated by the development of a pair of ribs on the first lumbar vertebra, and by an increase in the number of caudal (coccygeal) vertebræ from three to four, thus increasing the total number of vertebræ by one.

These variations are not confined to man, but occur in all the great classes of the Vertebrata. The assumption of lumbar characters by the last thoracic vertebra, and of thoracic characters by the first lumbar vertebra, in the rabbit is relatively not rare.

In the generative organs of earthworms and other worms homœotic

variation is known. As already stated the ovaries in *Lumbricus* and *Allolobophora* are normally a single pair, and are situated in the 13th segment. But an instance of a *Lumbricus turgidus* having an extra pair of ovaries in the 14th segment is described, and another as having an extra ovary in the right side only of the 14th segment; and in *L. purpureus* an extra one in the left side only of the 14th segment. A species of *Allolobophora* is described as having seven pairs of ovaries, situated in the 12th, 13th, 14th, 15th, 16th, 17th, and 18th segments. In all instances only one pair (the normal ones) of oviducts are present.

Variations in other parts of the genital organs, such as the spermathecæ, genital pores, &c., are also recorded. In some cases the spermathecæ of one side may be one segment in front of the normal one, those on the other side occupying their usual position.

In a large number of Mammalia (pigs, rabbits, dogs, cats, &c.) the mammary glands are arranged on two lines converging towards the inguinal (pelvic) region. The number of glands is variable, but they are usually the same on both sides. But not infrequently the number of mammæ on either side is different, and in these instances the paired nature is usually interfered with for most, if not all, of the glands. In the cow the normal number of teats is four and about equal in size, but not infrequently there are six, of which four are large and two are small and situated posteriorly to the others. In the dog the number of teats may vary from seven to ten pairs, and, as a rule, the greater the number of teats the greater is the numerical variation to which they are liable. In pigs the number may vary from six to eight pairs, and frequently there may be eight on one side and seven on the other, or there may be six and seven on either side respectively; in cases where the symmetry is thus destroyed the paired nature is also lost, since the second mamma of one side will lie in a plane alternating with the second and third of the other side, and so on.

Among elephants, Sirenia (sea-cows), many Lemurine monkeys, bats, apes, and man, the mammary glands are confined to the thoracic region of the body. In some Lemurine monkeys they are distributed, as in dogs, cats, pigs, &c., along the thoracic and abdominal regions, but in a few others, those in the latter region are undergoing retrogression and are in the course of disappearing, so that these monkeys only possess two functional mammary glands, in correlation with which they only produce two young at a birth. Now this latter condition is that of the apes and man. Not infrequently, however, both man and

woman exhibit the possession of more than a single pair of mammary glands. In most cases the supernumerary teats are situated below the normal ones, but sometimes they occur above them. Whenever they occur they are always so situated that they lie on two lines converging towards the inguinal region, that is, they occupy the same position as those of the functional glands in dogs, pigs, and most of the Lemurine monkeys. All degrees in perfection of development are observable in these supernumerary glands ; they may be fully formed mammæ with nipples, and capable of function in the female, or they may be nipples only, with no glandular tissue, or they may be lumps of mammary tissue without nipples or ducts ; in the male, cases are known where they are represented by nothing but a more or less deeply pigmented patch surrounded by an areola of hairs like those of the normal pair. A human female has been known with four pairs of supernumerary glands, three above and one below the normal pair, and from these milk oozed when the child was being suckled. In the case of man an instance is recorded of the possession of three pairs of supernumerary glands, two below and one above the normal ones ; of these, the one above and the lower of the two pairs below the normal ones are represented by pigmented spots with areolæ, while the pair next below the normal ones are represented by distinct though small teats with areolæ. Supernumerary teats have been observed in the Macaque monkey, in *Cercopithecus*, and in the orang-utan.

The possession of many teats constitutes a condition termed **polymasty**, and that of the possession of a pair of teats **bimasty**. The variations of this organ which occur in man may be said to tend towards polymasty.

The few facts which have so far been described show clearly enough that organisms do vary, and that some of these variations may be of a complex nature. At present our knowledge of any particular kind of variation is very meagre, and it would be unprofitable to attempt to discuss the causes of such variations. But in a few cases a sufficiently large number of observations have been made to enable us to deal in a mathematical way with them, and as far as they point the road to any conclusion it is that they are fortuitous and accord with the 'laws of chance.' Now events which accord with the laws of chance are simply those which happen under conditions of which we are ignorant. If we toss a penny the chances are equal that the tail surface of the coin will be uppermost as frequently as the head surface ; and we say that in a given throw it is a chance

whether the 'head' or the 'tail' will be uppermost. If we knew all the conditions which governed the movements of the penny we could predict of any particular throw which surface would be uppermost,

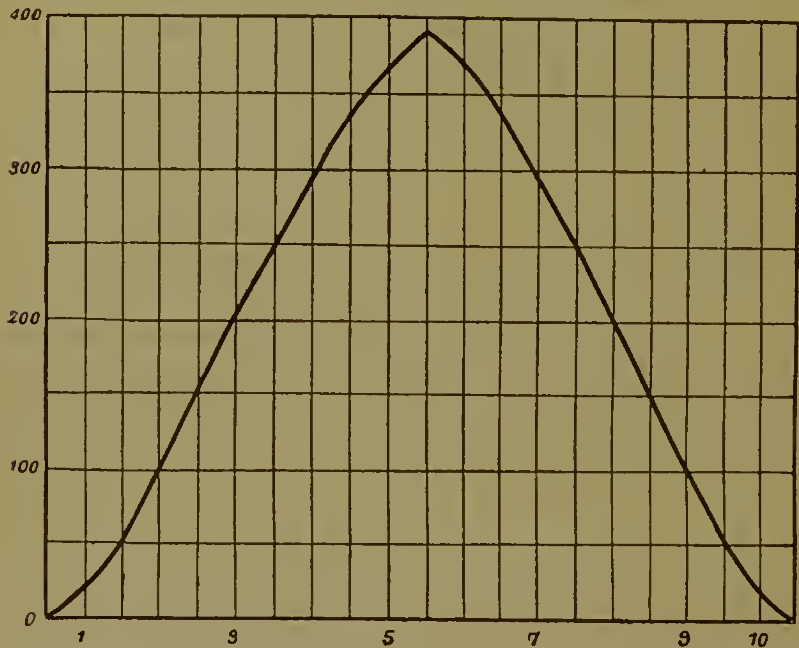


FIG. 99. A Normal Curve of Frequency of Error. In this curve the abscissæ (horizontal row of figures) indicate the extent or degree of the variations, as measured in terms of some chosen unit, such as millimetre, inch, or foot. The ordinates (vertical row of figures) indicate the frequency of the variations as determined by the number of the individuals measured. Thus in the figure the curve tells us that there are one hundred individuals who possess a given organ of two millimetres (if a millimetre is the unit adopted) in length, and it tells us further that there are also one hundred individuals who have that organ developed to nine millimetres in length. Or that there are two groups, each of 250 individuals, who have it developed to 3·5 and 7·5 millimetres in length respectively. It also shows us that the majority (390) of the individuals investigated possess the organ of 5·5 millimetres length, and that the two extremes of variation are 0·5 millimetres on the one side and 10·5 millimetres on the other. That is to say, that the greater number of individuals have the organ developed to the mean degree. But between these two extremes and the mean there are all possible gradations, so that the curve is a *continuous* one with no great gaps or indentations. And, moreover, it also shows us that the variation on one side of the normal does not tend to vary more than on the other, so that there is no greater tendency for the given organ to become larger than there is for it to become smaller, and so the curve is *symmetrical*; that is, its apex (modal point), if projected downwards, would lie at a point exactly in the middle of the base line.

Such a curve as this would result if the frequencies of a number of chance events (such as the frequency with which, say, the three dots on each of twelve dice would be uppermost in a sufficiently large number of throws) were recorded in this form.

and it would be no longer a matter of chance. But our ignorance of these conditions does not make the throw of the coin anything else than what it is, and our statement that it is governed by the laws

of chance does not make the conditions which govern it any different from those laws which control other falling bodies, such as planets, the movements of which we can accurately predict. The laws of chance, therefore, are the same as other natural laws, but they are acting under conditions of which we know little or nothing. The student, therefore, must not be misled by the expression 'laws of chance,' and believe that they are laws independent of, or different from, other natural laws; they are natural laws acting under conditions, of the nature of which we are ignorant.

If we examine any phenomena that are said to happen according to the laws of chance, such as the games of dice, roulette, &c., and tabulate the results, such as the frequency with which a given number of dots occurs in a given number of dice thrown a given number of times, and express them in the form of a **curve of frequency** (Fig. 99), there will be obtained a normal curve, the apex of which projected to the base (line of abscissæ) will lie midway between the extremes of its base (Fig. 99).

It can be shown that, in those cases of animal variation of which there are a sufficient number of observations, if the results are expressed in the same way a very similar curve is obtained. Francis Galton has shown this to be the case with the stature of individuals in a community. It is a matter of common observation that in a given community some individuals are short, some tall, and some medium in height; that is, the character of stature is a variable one. Now if a large number of persons be measured, and the results expressed in a graphic form, in which the ordinates (vertical column of figures) will indicate the number of people measured and the abscissæ (horizontal column of figures) their various heights, it is found that a normal curve of frequency of error is the result (Fig. 99). This curve expresses that the majority of people in that community are of the medium height, and that approximately there are an equal number of persons shorter or taller than this. In other words, the variation of stature may be on either side of the mean, or variation in either direction is equally probable. In this instance the curve is symmetrical, that is, the apex lies immediately above the middle of its base, and it indicates the mean height of the individuals of the community. But there are variations which, when plotted in this way, do not give a symmetrical but an asymmetrical curve.

Professor Weldon has recently been engaged in an investigation on the variation which shore-crabs show in virtue of the ratio which

the antero-lateral margin of the carapace bears to its length. He has found that there is an appreciable variation, and when the results are arranged in the form of a curve it is found that this is not symmetrical, for the range of variation is greater on one side of the mean than on the other. It is obvious that if a carapace with an antero-lateral margin having a given ratio to its length represents the mean, if variation occurs at all it may vary equally on either side of this mean, and produce an approximately equal number of crabs with smaller or larger carapaces, expressed in terms of the ratio of the antero-lateral margin to the length of the carapace, or it may vary more to one side of the mean than the other, producing a greater number of smaller or larger carapaces according to which side of the mean its range of variation is greatest. And the case of the shore-crabs of Naples, investigated by Professor Weldon, is of this nature, for the range of variation is greater on the side of the mean indicated by the larger measurements than it is on the other, and the curve of frequency is consequently asymmetrical.

In the cases of variation thus far considered, and treated mathematically, the curve of frequency is a single-apex one, because in the characters investigated the majority of individuals possess it, not in the highest or lowest of its extreme development, but in its mean. But it can be easily seen that if the individuals of a species could be arranged in two numerical groups in respect of a given character, in which one group would exhibit the character in its smaller development and the other in its greater development, then the mean of that character would be possessed by only a few of the individuals, and the resulting curve would be one with a double apex (Fig. 100).

Bateson (to whose monumental work on variation the student is referred for further particulars) has shown that the forceps at the hinder end of the body of the male common earwig (*Forficula auricularia*) are of two kinds, which he terms ‘low form’ and ‘high form.’ The former are small and belong to the smaller males, and the latter are of unusual length and belong to the bigger males. A thousand of these earwigs were collected indiscriminately from the same locality on one day (only sexually mature animals being retained) and their forceps carefully measured to the nearest half-millimetre. When the results are grouped in the graphic form it produces a double-coned curve, which shows that one group of the earwigs (slightly the larger) are of the ‘low form’ and the other of the ‘high form.’ Only a very few are of the mean form; that is, have forceps neither ‘low’ nor ‘high.’

The curve indicating the result of such observations would be very similar to that of Fig. 100.

Bateson has proposed to term animals **monomorphic** in virtue of any character which gives a single-coned curve, and **dimorphic** when the graphic result of any character investigated produces a double-coned curve. Variations which when represented graphically produce

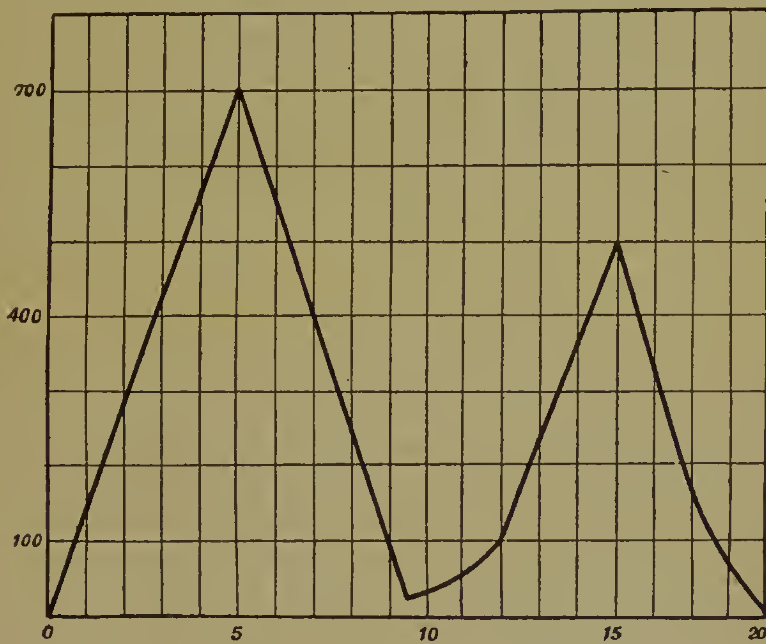


FIG. 100. A Curve of Frequency of Error showing Discontinuous Variation. The abscissæ indicate the degree of variation of an organ as determined by measurement and recorded in some chosen unit (millimetre, inch, or foot), and the ordinates the frequency of variation as determined by counting the number of individuals possessing an organ of a given length, &c. The curve shows that of the total number of individuals investigated with reference to the variation of some character or organ capable of arithmetical expression, 700 of them had the organ of 5 millimetres length, while 500 had it of 15 millimetres length. The number of individuals possessing it of mean development is very small, i. e. thirty. Hence the character or organ under investigation is varying in two directions, each diverging from the mean. In one direction it is tending to develop into a smaller one, i. e. of about 5 millimetres, and in the other into a larger one, i. e. of about 15 millimetres. The variations between the two extremes do not form a continuous series, but are arranged into two groups, so that it constitutes a *Discontinuous Variation*.

a double-coned curve are called by Bateson **discontinuous**, and those which give rise to a single-coned one, **continuous**.

Substantive variations (ante, p. 388) may be illustrated by various species of plants in which the flowers or other parts of the individuals are of different colours or different shades of colour. Thus various species of narcissus have individuals in which the flower may be a full yellow or a pale sulphur yellow, and in some species some

may be white. The same is true of tulips, but the colour range is different. Every one is familiar with the variety of colour which different individuals of the cat species exhibit, and in their colour-patterns also. There is also a great variety of colour and markings among one of the commonest British lady-birds. In the eye-colour of man there are certain types of colour which are common, while the intermediate types are relatively rare; and these eye-colours do not blend, for in a family some members will exhibit eyes of one type-colour and others of another, but none will show any colour that can be considered as a blending of the two. Colour dimorphism of this kind is common both among animals and plants; some beetles exhibit it in a well-marked manner, for in both sexes of the individuals of a species there may be two varieties of colour. Occasionally species of birds, that are characterized by a very definite and striking colour, will produce individuals of another colour equally striking; thus a case is known of the green-ring parakeet (*Palæornis torquatus*), which normally is almost entirely a brilliant and vivid green, being entirely canary yellow; it later developed a few green feathers.

In these few instances of substantive variation that have been described there are no intermediate types tending to connect or bridge over the gap between any two degrees of variation; the degrees of variation do not form a continuous series, in which the one passes gradually into another and so on, from one extreme to the other. There are gaps, and the variations are therefore **discontinuous**.

The student no doubt is beginning to wonder where all these dry and disconnected facts are leading, and what conclusion can be derived from them. No man living can say whither these facts will ultimately lead, any more than a man in mid-Atlantic can prophesy the whereabouts of the shore that any given billow will ultimately roll upon. The road of truth is a long one that will not be traversed in our generation or in the next; and probably in no generation, though they succeed one another in endless procession. Our duty is to traverse it as far as the resources of our age will allow, and to gain some idea, whenever possible, of the direction whence it trends.

We look around us on the living world and behold a manifold display of various kinds of animals and plants, rich in the variety of their structure, but almost richer still in the display of their remarkable activities. Man has examined, sorted, and classified them; he has divided them into kingdoms, phyla, classes, orders, families, genera, and species. But his classification is arbitrary and

ineffective, for not only does one naturalist regard as a species that which another holds to be a mere variety, or which another would claim to be of generic rank, but Nature herself cares nothing for it and refuses thus to be split into groups. We roam the hills and vales of Scotland and collect the 'Brown Argus' butterfly; we come to the southern pastures of England and we discover a butterfly very much like that of Scotland, differing only in the presence of certain orange spots on the upper sides of the wings, and in that the pure white spot of the under sides has a black centre. In virtue of these differences we decide that they are two different species, though in virtue of the similarity of other characters, such as the arrangement of the nerves in the wings, we include them in the same genus. We name the Scotch form *Polyommatus artaxerxes* and the southern English form *P. astrarche.* We visit the midland and northern counties of England, and we find forms that cannot be put in either one or the other species, for they are intermediate in character between them; obviously our division into species is purely artificial, a matter of convenience to naturalists, but as being expressive of absolute differences between organisms it is futile and misleading. True it is there are many species to-day that are not connected with one another, and between which there is no known connecting link. But it does not follow that there were no connecting links in the past, and if we could imagine that the central parts of England were to disappear beneath the sea or some other physical environment were to destroy the variety of 'Brown Argus' butterfly that connects the Scotch and southern English forms, there would be two distinct species with no connecting link between them; and yet we know that they are actually connected, and that changes of physical environment and alterations in the level of the land are facts that have been and still are. There is no reason for believing that the operations of Nature in the past were any different to what they are at the present, and there is therefore nothing to prevent us believing that, at one time or another in the various epochs of the world's history, all species were connected by every possible grade of connexion. Just what is happening with the 'Brown Argus' butterfly has probably happened with countless thousands of species that have lived or which are still living; the link or links that connected any two species have disappeared.

But none the less the fact remains that the living organisms of nature are diverse, that there are phyla, families, genera, and species innumerable. How came this diversity to be brought about? Have

all the different species and varieties, and all the subtle connecting links, been created by the fiat of a Creator? Or have they all arisen from a single speck of primordial jelly by a long process of evolution? This is a great question that has agitated the minds of men for untold generations, and is renewed with increased interest for every fresh generation that arises. Its answer is full of possibilities of the profoundest bearing upon human life and well-being, and all that can be done to lead us to the true answer should be done. The idea of creation is unthinkable; it does not answer in even a small measure the facts of life. If species have been created, why are they connected by every possible structural gradation? Why are animals that live a wholly terrestrial life possessed of organs of respiration and associated structures of a purely aquatic nature? Why has the horse one useful digit and two useless ones on each limb, and why as a variation do the useless ones tend to become useful? Why is it that man, in the course of his embryological stages, passes through conditions that characterize stages and permanent and finished structures of the lower Vertebrata? These are difficult questions very hard to answer, and cannot to-day be answered with certainty or finality. But this much is certain: the hypothesis of creation does not answer them, while that of evolution gives us an understandable and possible answer.

If evolution be true, then how and why came it to pass? It is just here that the study of variation may help us; for if it can show how species have probably arisen from one another, by demonstrating that by variation they are arising at the present, the road is clear for the answer to the question.

Biologists are divided into two great camps on the question of the 'Origin of Species.' There is the Lamarckian or older camp, and the Darwinian or newer one. The former asserts that organisms are profoundly modified by the necessities of their existence and the nature of their physical environment, and that these modifications are hereditarily transmitted, accumulated, and perfected with each generation. The Darwinian camp, on the other hand, asserts that variations are fortuitous, that they arise spontaneously from some inherent cause of which we know nothing, but that having arisen, they can be either advantageous or otherwise to the organism. If advantageous, then they confer a benefit and advantage upon the organism possessing them, which the others do not possess; and that therefore, in the struggle for existence, the former will survive and procreate their

species, and the latter will become exterminated. Thus Nature selects the fittest to survive and rejects the unfit, and hence to the Darwinian theory has been given the name of **Natural Selection**. Thus may be explained why organisms are adapted to their environment; not because, as the Lamarckians assert, Nature has indiscriminately moulded them to it, but because those not so adapted have become exterminated.

And if species have arisen according to the theory of natural selection, we want to know how and by what kind of variation they have so arisen. It is easy enough to take a series of species and to say this or that species could have arisen from a certain one or another, *if* this or that variation had taken place. But the word *if* can have no permanent abode in the edifice of science; for, actuated by the almost certain probability that the laws of the past have been what those of the present are, the question that our generation has set itself to solve is: How are species now arising through the agency of variation? in order that the theory of evolution and of natural selection may stand as inflexible truth, or be relegated to the limbo of exploded, though not necessarily useless, hypotheses.

INDEX

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THE END

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